



## A morphological review of tribes in Larentiinae (Lepidoptera: Geometridae)

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### Abstract

Tribes of looper moths (Geometridae: Larentiinae) are reviewed. The tribe Dyspteridini Hulst is reinstated (previously synonymous with the Trichopterygini Warren). A new subtribe, Aplocerina, is separated from the Chesiadini Pierce, and the group Ortholithinae Pierce is dealt with as Scotopterygini Warren, the sister taxon to Xanthorhoini. Morphological traits for 22 of 23 larentiine tribes represented in the Holarctic fauna are listed and illustrated. A taxonomy of the subfamily Larentiinae is proposed and supported, using morphological data based on chemical communication structures and male genitalia. A new combination is presented: *Melanthia mandshuricata* (Bremer), transferred from *Mesoleuca* Hübner (Larentiini)

**Key words:** Geometridae, Larentiinae, tribes, comparative morphology.

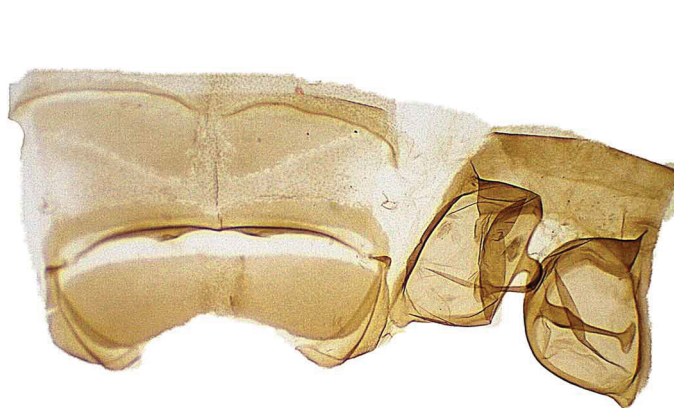
### Introduction

The subfamily Larentiinae comprises more than 6000 species worldwide. The present taxonomic structure of the subfamily is more or less traditional (see elaboration below). Heppner (2005) lists 18 tribes for Larentiinae, and 20 tribes are listed in the Forum Herbulot homepage (<http://www.herbulot.com>) (Heterusiini and Erateinini are added to those listed by Heppner). Some of the tribes have never been described but characterized merely by names of their typical genera. Rapidly developing molecular systematics has yielded the first data to aid in larentiine taxonomy. Several representatives of larentiine tribes were used for outgroups in projects by Yanamoto and Sota (2007), Snäll et al. (2007), Strutzenberger *et al.* (2010), and Sihvonen *et al.* (2011) consider 38 taxa from 15 tribes (and five taxa unassigned to a tribe; any taxonomic analysis of southern hemisphere larentiines must be preceded by a description of genera). The aim of the analysis presented herein is to compare morphological characteristics of larentiine tribes and monophyletic groups at the genus level within family-group taxa, broadening the scope of study to all biogeographical regions by describing the spatial distribution of the male complex characters e.g., coremata, labides and valval ornamentation.

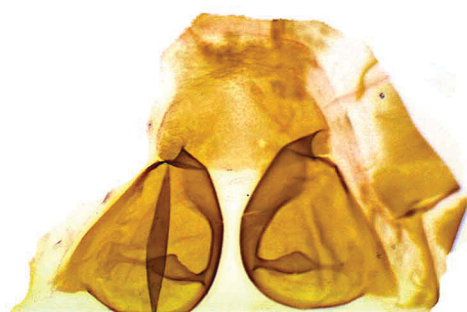
Family group names in *Geometridae* were introduced in the 19th and early 20th centuries, first by Hübner, followed by Duponchel (1845), Stephens (1850), Guenée (1858), and then by Meyrick (1892), Warren (1893, 1894) and other authors. The usage of genus-group and family-group names was at that time subjective (based on overall similarity of moths, or head, antennae, leg characters etc.) and not always consistent. For example, Stephens (1829) listed *Chesias* Treitschke with its two species as a genus among other geometrid genera. In a later work, Stephens (1850) used Hübner's genus name *Eucestia* Hübner for these species, synonymised *Chesias*, but introduced the family group name *Chesiadi* for three related genera. Pierce (1914) was the first to combine *Chesias* Treitschke and Chesiadini validly.

The family group name *Larentites* was introduced by Duponchel (1845). The subfamily Larentiinae was diagnosed by Holloway (1997: 99) according to the wing pattern, “each fascia in forewing tending to be multiple...and meeting the dorsum at right angle. ...the species rest with the forewing mostly or wholly covering the hind wing (Common 1990). Minet (1983) defined Larentiinae by the hammer-headed shape of the ansa but this trait characterizes tropical groups of Sterrhinae as well”. The ansa is apically triangular-truncate rather than hammer-shaped in

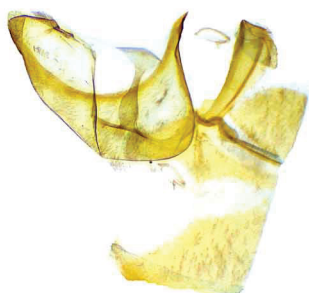
some boreal groups of Sterrhinae (compare Fig.1 for *Idaea* (Sterrhinae) and Figs 2–4 for Larentiinae) but hammer-shaped in tropical genera e.g., *Zythos* Fletcher. Accordingly, the shape of the ansa is a symplesiomorphic character shared by Sterrhinae and Larentiinae. Usually the larentiine forewing venation is characteristic in veins Rs and M<sub>1</sub> stalked or, if separate, M<sub>1</sub> proceeds in line with the anterior margin of the discal cell (Öunap *et al.* 2005, 2008). The monobasic tribe Lythriini was recently moved from Larentiinae to Sterrhinae on the basis of a molecular-phylogenetic analysis (Öunap *et al.* 2005, 2008). A subsequent large-scale molecular phylogenetic study of Geometridae (Sihvonen *et al.* 2011) proved that this rearrangement was correct as *Lythria* again clustered within Sterrhinae.



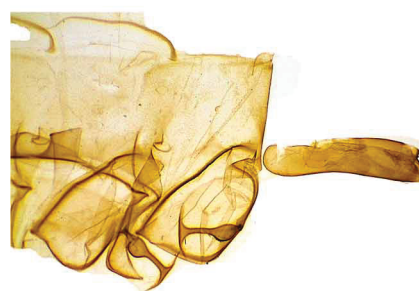
1 *I aversata*



2 *O internata*



3 *R sp.*



4 *T sabaudiata*

**FIGURES 1–4.** The shape of ansa in Sterrhinae and Larentiinae. 1, Sterrhinae (*Idaea aversata* (Linnaeus)); 2, Larentiinae, Trichopterygini (*Oulobophora internata* (Püngeler)) (Turkey); 3, Trichopterygini (*Rhopalodes lecorrei* Viidalepp) (Fr. Guiana); 4, Rheumapterini (*Triphosa sabaudiata* (Duponchel)) (Crimea).

Earlier authors (Hübner, Stephens, Warren, Meyrick and others) named genus groups according to typical genera without concise descriptions. Herrich-Schäffer, Spuler, Hulst, Comstock and others initiated the usage of the venation of wings in genus-level taxonomy. Pierce (1914) was one of the first authors who not only analyzed characters of genital structures but also used them in geometrid systematics to combine taxa based on their anatomical similarity, and to substantiate family group names. Based on the absence or presence of a male genitalia sclerite, the gnathos, he divided geometrids into two larger groups, *Gnathoi* and *Agnathoi*, separating eleven genus groups (as subfamilies) in the first, and fourteen in the second (Pierce 1914). The author made use of Prout's term *coremata*: "The seventh segment ... is sometimes highly developed, being produced on either side as an extensile pouch or bag clothed with hairs, and bearing a spiracle. These bags are *The Coremata* (Wytsman Gen. Ins. Hem. p. 6), to a form which I have referred to ... as occurring on the ninth segment in the *Eupitheciina*" (Pierce 1914 pp. 28–29).

The presence of coremata like that described is mentioned in characters' spectra of *Epirrhoinae* and *Ortholithinae*. Analogous hair pencils on wings and legs were described much earlier. The usage of genus-group and family-group names was subjective or in brief descriptions of species that are nowadays placed in xanthorhoin genera (Pierce 1914). However, the presence of coremata on the seventh segment (instead of the ninth) is mentioned for several genera outside these three subfamilies, i.e. for *Collix* Guenée and *Eulype* Hübner (*Anticollix* Prout, *Rheumaptera* Hübner as understood in recent times) of his Eupitheciinae, and for *Euphyia* Hübner of his Melanthiinae. The synthetic approach by Forbes (1948) explicitly grouped genera with large coremata on the seventh segment of abdomen of male in his tribe Xanthorhoini, thereby combining species of *Euphyia* Hübner with *Xanthorhoe* Hübner. It must be mentioned that Forbes grouped numerous genera with and without coremata as well as other structural peculiarities absent in males, into the first larentiine tribe, Hydriomenini. Forbes' system is basically followed by later workers on geometrid taxonomy in North America, although McGuffin substantiated the separation of the tribe Mesoleucini (here synonymized with Larentiini).

When rearranging genera of geometrid moths according to their genital characters for a checklist of the fauna of the former USSR (Viidalepp 1976–1979, 1996), it became obvious that Herbulot had done this earlier. Herbulot's (1961–1963) approach to the system was analytical, again, based on comparative morphology and resulting in the separation of 14 tribes within larentiine geometrids. Herbulot's arrangement has strongly influenced the treatment of larentiines in the Palearctic fauna.

Holloway was the first to try to generalize the treatment of larentiines worldwide based on detailed knowledge of Indo-Australian genera (Dugdale 1980; Craw 1987; Holloway 1997; Schmidt 2002; Abraham *et al.* 2001) and the synthesis of available morphological, ecological, and behavioral data. Holloway (1997) wrote: "The presence of a large pair of coremata just distal to the eighth segment in the male abdomen appears to be the most constant feature for this tribe, though the occurrence of a calcar ... is an additional diagnostic feature that is characteristic of many of the component species... The calcar-bearing taxa fall within the broader concept of Xanthorhoini defined above on characteristics of the pair of large coremata associated with the eighth segment. The male antennae tend to be bipectinate."

## Material and Methods

For a comparative morphological study, moths from the collection of the Estonian University of Life Sciences (Tartu, Estonia) (former Institute of Zoology and Botany of Estonian Academy of Sciences, IZBE) and of the Estonian Museum of Natural History (Tallinn) were used. The genera and subgenera investigated are listed in Appendix 1. Results of comparative morphological study were formerly used for keys to genera and species of butterflies and moths of the Estonian fauna (Viidalepp & Remm 1996), to geometrid moths of Central Asia (Viidalepp 1988) and the Soviet Far East (Viidalepp 2005). Examination of genitalia followed the procedures described by Hardwick (1950). Moths were photographed with a Canon 350D camera. Genital slides were photographed with a Leica 3C digital camera attached to an Olympus SZX12 stereomicroscope. The digital images were enhanced using Adobe Photoshop Elements 7 and combined into plates. The review here is based prevalently on Holarctic material.

## Systematics

**Morphology.** There are numerous reviews of the morphology of Geometridae in the literature. The most recent ones are those by Common (1990), Holloway (e.g. 1997, 2001), Minet and Scoble (1999), Hausmann (2001), Scoble (1992), but detailed reviews by Pierce (1914), Forbes (1948), and Okagaki *et al.* (1955) remain important, and handling of some subordinated groups is in Petersen (1909) to Sihvonen and Kaila (2004). A large amount of morphological data has been accumulated that have to be systematized for a background of the developing molecular systematics. The morphological basis of the system of the subfamily Larentiinae in use is rather obscure. The morphological terminology used follows Hausmann (2001), and some traits characterising larentiines are discussed below.

**Head.** The head is approximately rounded in shape, the frons is usually flat and covered by overlapping flat scales. Extra sclerites laterally to the clypeus characterize Operophterini (Forbes 1948; Snäll *et al.* 2007), genal

sclerites enlarged and projecting angulate towards clypeus, are a peculiarity of Chesiadini. Eyes are often smaller in day-active groups. The frons is usually vertically shorter than the diameter of the eye, but enlarged, projecting and rounded in some Asthenini genera, while in *Aplocera* Stephens the frons is slanted towards the palpi and is also estimated to be longer than the eye diameter. In Xanthorhoini, frontal scales are gathered into a conical tuft oriented towards the palpi.

Labial palpi are usually relatively short in larentiines except in some cases in Cidariini (Choi 1997), and are long, pointed and sickle-shaped in Lythriini (Hausmann 2001: 53), which has been recently moved from Larentiinae to Sterrhinae (Öunap *et al.* 2008). Larentiine antennae are mostly filiform, segmented and cylindrical (Hausmann 2001: Fig. 77) or flattened (loc cit, Fig. 79); in species with bipectinate antennae each segment bears two rami (loc cit, Figs 81–82), in species with quadripectinate antennae—two pairs of rami (Cidariini: *Protothera*; cf. Viida-lepp and Kostjuk (2005); Choi (1997). The chesiadiine genus *Amygdaloptera* Gumpfenberg and *Pljushtshia* Viida-lepp & Kostjuk (Cidariini) are exceptional in reduction of inner side pectinations, having unipectinate male antennae (Hausmann 2001, Fig. 84). Some trichopterygine genera have male antennae unusually stout, others have antennae subapically dilated.

Chaetosemata are often small rounded patches located posteriorly to antennal bases, but enlarged in *Triphosa* Stephens, connected by a continuous row of setae in Asthenini (*Discoloxia blomeri* Curtis, Fig. 7). Eudulini and Stamnodini (Figs. 5, 6) possess large chaetosemata across the vertex.

Relatively rare cases of the reduction of haustellum are accompanied by shortening of labial palpi (Operophterini, but also *Celonoptera* Lederer), reduction of wings—by diminishing thorax and abdominal tympanals (Operophterini). The reduction of the frenulum occurs within some Neotropical moths, e.g. Erateinini. Quite possibly, the genus *Erateina* sensu Doubleday is composite (Figs 84–88).

**Wings.** Wing shape and facies were used in taxonomy of moths in the 18th and 19th centuries, and only late 19th century works by Herrich-Schäffer, Spuler, Comstock, Hulst and others have shifted the taxonomy regarding the differences in venation of wings, structure of palpi and legs. Original descriptions of larentiine genera most often appear to be based on characters which reflect different stages and variations in the framework of an overall trend of costalization of wing venation in insects, on different combinations of anastomoses in the costal part of the wing, and on the shortening and direction of the discal vein. The costalization of venation is associated with aerodynamic characters of flight; as an overall trend, it proceeds independently and in parallel in various groups, and therefore, the treatment of such modifications as synapomorphies is often questionable. Based on autapomorphies, such genus definitions are not suitable for parsimony analysis (cf. Sihvonen and Kaila 2004, Fig. 1). Sexually different venation of the hind wing costal area is shared by Trichopterygini and Chesiadini. As usual, larentiine venation of forewing is characterized by the presence of two accessory cells between radial veinlets ( $R_1$  and  $R_2$  branch out separately) and only in the subtribe Chloroclystina Mironov,  $R_1$  and  $R_2$  arise stalked and  $R_1$  anastomoses with Sc, while  $R_2$  anastomoses with the stem of  $R_{3+4}$  or  $R_{3+5}$ . For comparison some genera of Rheumapterini also possess one accessory cell only in forewings. Some special wing modification trends appear in Trichopterygini such as reduction or splitting of male hind wing anal area.

Some cidariine genera have sexual modifications, such as tufts of hairscales on fore- or hind wings as genus-level (*Photoscotosia* Warren) or species-group characters, and there are one Palearctic and one Nearctic species of *Hydria* Hübner (*H. undulata* (Linnaeus) and *H. prunivorata* Ferguson, accordingly) with a patch of specialized glossy scales at the anal margin of the hind wing. Some trichopterygine genera, such as *Sauris* Guenée have the distal margin cleft and/or hair tufts of the forewing present to the modified anal region of hind wing. *Hammaptera* Herrich-Schäffer is outstanding because its hind wing anal area is thickened and densely covered with hairscales.

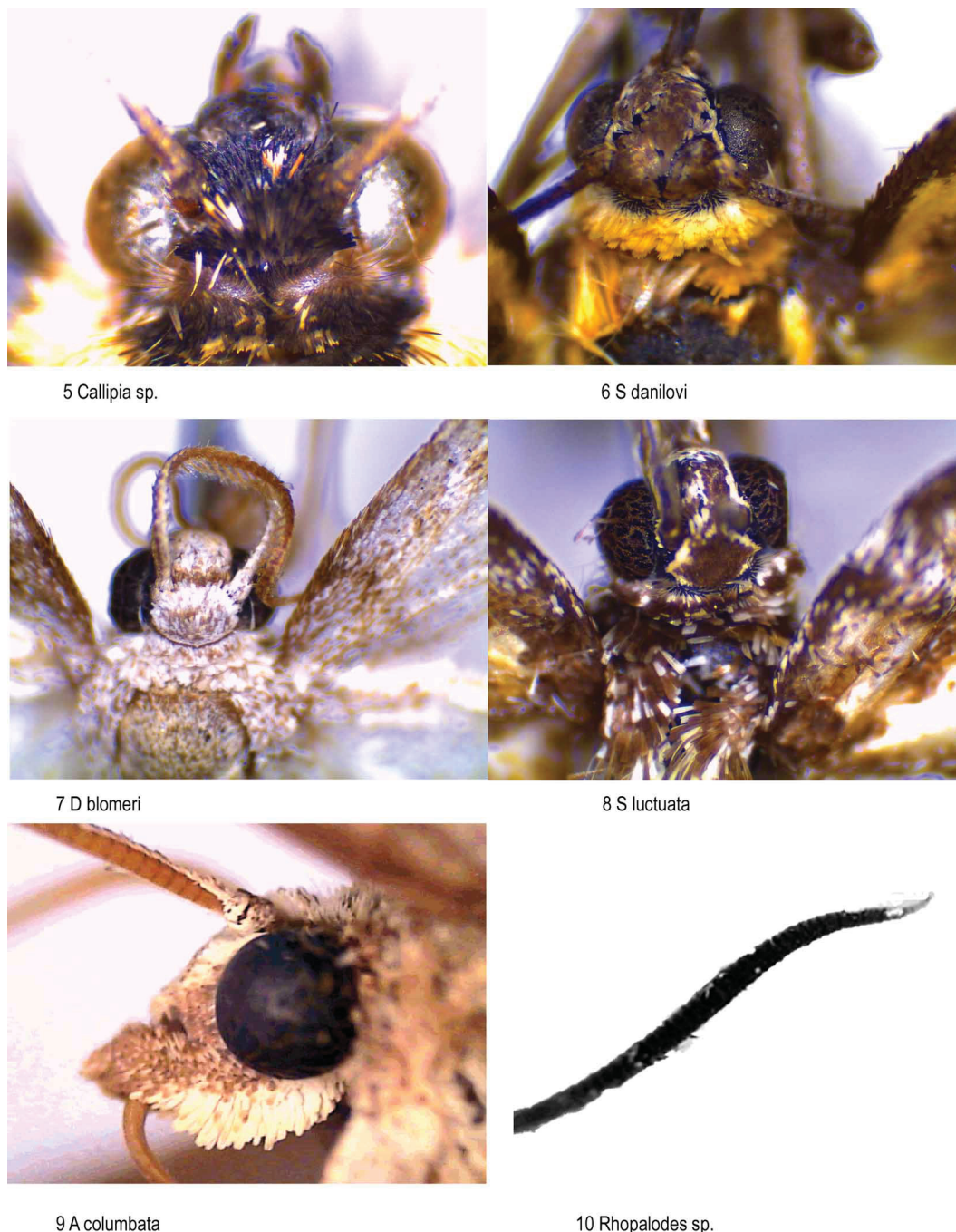
**Thorax and abdomen.** The larentiine metathorax usually bears a low tuft or a pair of tufts of erect scales (Forbes 1948). The dorsum of the thorax is usually smooth or delicately tufted, but peculiarly hunched in two genera: *Pelurga* Hübner (Larentiini) and *Pareulype* Herbulot (Rheumapterini). Choi (2006) has shown that the genera are not closely related despite the similarity in their wing maculation.

The dorsum of abdomen is smoothly scaled in larentiines. Some cases of extremely long abdominal segments are known for New Zealand, Australian and Neotropical Trichopterygini (Fig. 72), but usually the abdomen is not longer than wings (Fig. 86). The last tergite is thickened in arid environment chesiadiines, sometimes provided with a rough supporting hunch in some *Lithostege* species (Figs 31, 32).

There are hair pencils supposedly associated with the scent organ lateroventrally on the fourth segment in *Ecliptopera* Warren (Cidariini). Spreadable coremata, used in pre-copulatory chemical communication between



sexes, are usually associated with segments A7 and A8 in males of the tribes Xanthorhoini, Euphyiini, Rheumapterini, Melanthiini and Cataclymini, while in Eupitheciini hair tufts are attached to valvae bases (or to the ninth segment). In case of the presence of coremata, tergites and sternites A8, or even A6–A8 are partly membranized (except for Eupitheciini). A detailed comparison of the coremata of the groups listed (below) probably makes questionable the use of this character as a synapomorphy of the genera grouped within Xanthorhoini sensu Holloway 1997). The richest spectrum of scent distribution structures, especially those associated with dissclerotization of posterior abdominal segments in male, is represented in the faunas of the southern hemisphere.



**FIGURES 5–10.** Heads in Stamnodini, Eudulini Asthenini and Trichopterygini. 5, Stamnodini (*Callipia* sp.) (Bolivia); 6, Stamnodini (*Stamnodes danilovi* Erschov) (Touva); 7, Asthenini (*Discoloxia blomeri* (Curtis)); 8, Rheumapterini (*Spargania luctuata* Denis & Schiffermüller.); 9, Chesiadini (*Aplocera columbata* (Mentzer))(Crimea); 10, Trichopterygini (*Rhopalodes lecorrei* Viidalepp), antenna (Fr. Guiana).

Hair tufts, which supposedly act in scent distribution and pre-copulatory communication between sexes, may be located on fore-, mid- and/or hind legs of a tropical Trichopterygini (Dugdale 1980; Holloway 1997). Two Holarctic trichopterygine genera, *Pterapherapteryx* Curtis and *Lobophora* Curtis, as well as *Oulobophora* Herrich-Schäffer from the Mediterranean region have long and compact pencils of hair scales at the base of male hind tibia, concealed in a rim of a projection of sternite A2 when not in use (Fig. 73). Another trend occurs in Rheumapterini: reduced hind tibial spurs and thickened basal tarsal segment are associated with long and thick vestiture (Figs 69, 70).

Another specific modification, the occurrence of an apical spine to foretibia, is synapomorphic for *Aplocera* Stephens and related genera. The character is further modified in another subtribe, Chesiadina, where foretibia is short, flat and bidentate apically, the forefemur short and thick—the entire foreleg forms a grasping tool to emerge from pupal skin in a hard ground. The trend seems to be a synapomorphy for the tribe Chesiadiini.

**Male genitalia.** Male genitalia of larentiines are relatively simple, characterized at the subfamily level by the loss of gnathos (except some genera of Trichopterygini) and the reduction of socii resulting in a shift of scaphium abductor musculature from socii to uncus (Sibatani *et al.* 1947; Ogata *et al.* 1957; Kuznetsov and Stekolnikov 2001).

The male genital armature is organized based on modified sclerites of the ninth and tenth abdominal segments. The derivatives of the ninth tergite and sternite, named, accordingly, tegumen and vinculum, are jointed or fused to a ring. Both parts are often almost equal in measure, but sometimes one or the other dominates e.g., vinculum within Asthenini (Figs 53, 54, 56) and Melanthiini (Figs 58, 59, 61). Other modifications of the male abdominal ninth segment of taxonomic value are: the vinculum dorsal branches dilated medially, more or less triangular in shape, with valvae jointed to the posterior margin of the thickening in Larentiini (Fig. 101).

Supposed remnants of the reduced tenth and eleventh abdominal segments—uncus, is attached to the posterior margin of tegumen, socii are inserted at uncus base, and gnathos jointed to the dorsal part of tegumen ventral to the base of the uncus.

Socii are absent in most Larentiinae, but present as small irregular pads at the base of the uncus in *Scotopteryx* Hübner (Figs 113, 115, 116) are supposed to be remnants of reduced socii. The paired, heavily sclerotized, long and tapered projections from the posterior side of tegumen, which are the peculiarity of two species of the genus *Solitanea* Djakonov (the tribe Solitaneini Leraut) can be identified neither with socii nor with gnathos.

The uncus as a pointed hook jointed to the distal margin of tegumen is a ‘normal’ condition in Lepidoptera, but there occur numerous secondary deviations from this condition. The eupitheciine uncus is usually dorsoventrally bi-pointed at tip in most Palearctic species (Mironov 2003) but often simply pointed or reduced in Indo-Australian (Holloway 1997) and Neotropical (Rindge 1987) genera. In a small group of Phileremini, the ring of the ninth segment (tegumen + vinculum) is reduced in size but the uncus tends to be very long and thin, needle-shaped (Fig. 74).

The uncus is membranized and weak in Melanthiini, skinny, without a sclerotized distal projection, setose dorsally (Fig. 58). It is short and weak also in some species of the Palearctic genus *Scotopteryx* Hübner, but shortly produced posteriorly and accompanied by reduced pads socii, and, as a rule, reduced in asthenine genera (Xue and Scoble 2002)(Fig.116). In the case of the tribe Melanthiini, the absence of an uncus hook is functionally replaced by a well derived and armed anal tube (falces, as termed by Vojnits (1987) for Eupitheciini); it is different in other tribes.

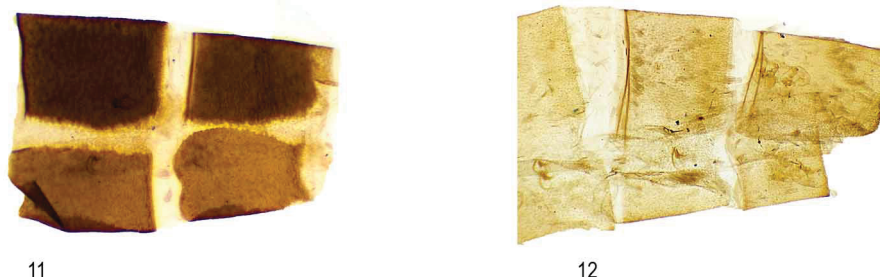
While membranized, weak, flat and setose in Melanthiini, the uncus is heavily sclerotized, flat, of trapezoidal, semicircular or triangular shape within the tribe Rheumapterini, incl. Neotropical and Holarctic genera (Figs 62, 64). However, a ‘normal’, hooked uncus also occurs in some associated East Asiatic taxa (Xue and Zhu 1999) of the Rheumapterini.

A heavily sclerotized dome-shaped uncus (Figs 62, 64) is a peculiarity of the widespread genus *Euphyia* Hübner (tribe Euphyiini) also from the Neotropical and Holarctic regions: as a trend, a possible synapomorphy for Euphyiini and Rheumapterini, but very little is known about the variability of this character in Neotropical genera allied to *Euphyia*.

Last but not of least significance, the uncus is flat, projects distally long and is pointed bifid in *Paraplaneta* Warren, while the projections are distally rounded and basally fused in its Mediterranean sister-genus *Cataclysm* Hübner (Viidalepp 2009).

According to Pierce, the genitalia are withdrawn into the last abdominal segments, under natural conditions. In simpler cases, both the abdominal tergites and sternites appear to be of rectangular or trapezoidal shape, of equal

length and width, and connected by thinner, less sclerotized pleural membrane (Fig. 11). Usually, sternites are more slender than tergites.



**FIGURES 11–12.** Body shape in Larentiinae. 11, Last abdominal sternite and tergite of equal length; 12, the sternite A8 shorter than tergite A8.

**Valvae ornamentation.** An observation of modes of valval ornamentation indicates that Chesiadini only seem to have a harpe, short in the subtribe Aplocerina and projecting long in Chesiadina. The following tribes have both costal and saccular ornamentations to valva: the aplocerine genera of Chesiadini, Scotopterygini, Cataclysmiini, Erateiniini, Rheumapterini with Triphosini, Melanthiini, Therini Pierce (synonymized with Cidariini by Choi 1997) and some Trichopterygini. Asthenini stand out having the saccular projection only, Xanthorhoini—with the valve costa projecting and sacculus reduced. The Cidariini, Stamnodini and Hydriomenini have sacculus completely fused to the less sclerotized valvula, while costa is moderately chitinized and demarcated against valvula by a ribbon-like lacinia costalis or a short furrow (Cidariini, Philereimini).

**Coremata.** The presence of male abdominal coremata in larentiine geometrid moths is associated with the modification of last abdominal segments (Fig. 130). Pierce (1914) found the structures, which Prout (1912) named "coremata" in the context of Geometrinae genera, present in some of his 'subfamilies' Geometrinae, Ennominae, Caberinae (Gnathoi), as well as in Acidaliinae, Eupitheciinae, Melanthiinae, Philereiminae, Epirrhoinae, Ortholithiinae and Xanthorhoinae of the group Agnathoi. The coremata were found to be associated with the ninth segment, attached to valvae in Agnathoi and Eupitheciinae, but associated with the seventh segment in most subgroups of Agnathoi Pierce 1914.

Petersen (1909) defined eupitheciine coremata as androconial structures associated with pheromone glands and used for pre-copulatory chemical communication at species level. Earlier, tufts of specialized hairscales or androconial scales on wings were described (many authors). Later on, long hair tufts attached to valvae were described in southern hemisphere trichopterygines (e.g., Dugdale 1980; Parra 1996), and in *Hagnagora* Druce the valval vestiture may also be associated with pre-copulatory behaviour (Fig. 149). Holloway (1997) tends to combine together in Xanthorhoini all the genera with coremata attached to the seventh abdominal segment in the male, and in Eupitheciini the genera with coremata at the ninth segment.

A simple (or simplified?) structure of coremata is developed in *Scotopteryx* (*S. perplexata*), in which the short eversible membranes are associated with the reduced in length segment A7, while sclerites A8 remain relatively unmodified (*S. chenopodiata* (Linnaeus), Fig. 114). In typical cases, segment A7 is membranized distally, the tergite shortened to a bow-shaped sclerite, and the proximal edge of the sternite remaining as a chitinous stripe. Tergite A8 is reduced to its anterior edge which is provided with a (smaller than usual) rectangular flap, the corresponding sternite being diminished to the stripe-shaped anterior margin.

This condition is shared by the genera classified into Xanthorhoini, Cataclysmiini and Euphyiini. On this ground plan, variations exist, embracing larger or smaller genus groups. The southern hemisphere genera of Xanthorhoini often have sternite A8 heavily chitinized and of protruding V-shape (*Chrysolarentia* Butler, Figs 136, 137). In Cataclysmiini (*Cataclysmia* Hübner, *Paraplaneta* Warren, *Phibalapteryx* Curtis, Fig. 104) there are a pair of arrow-shaped sclerites at bases of extensile parts of coremata (Fig. 105). Euphyiini differ in fusion of the stripe-like remnants of the last tergite and sternite into a ring bearing a rectangular dorsal and another, keel-shaped ventral lap (Fig. 119).



Chemical communication is widespread among Lepidoptera. There is a wide selection of means to distribute sexual pheromones and other odours (Kristensen 1999). Special structures for pheromone production and distribution may be localised on the wings of moths (e.g. in Cidariini, Trichopterygini, Erateinini and in some Neotropical groups of moths not yet assigned to a tribe), on legs (Trichopterygini, Rheumapterini). Hair tufts, locks and modified hairscales attached to genitalia (Erateinini, Larentiini, Trichopterygini, Hydriomenini, Stamnodini) occur in other subfamilies, but their similarity in Stamnodini, Hydriomenini and Larentiini points to homology. The presence of simpler hair tufts attached to the fourth abdominal segment is rare in Cidariini (e.g. *Trichobaptia* Prout) and on some segments in Melanthiini. The presence of pairs of extensile coremata at bases of valvae attached to the last abdominal segment in a position shared by Eupitheciini, Asthenini, Rheumapterini and some Neotropical genera not assigned to a tribe appears to co-occur with different modifications of the last sternite and tergite as described above.

Again, the position of extensile coremata at, and membranization of abdominal segments A7 and A8 in Cataclymini, Scotopterygini, Euphuini and Xanthorhoini seems homologous, but genital capsules are different enough in each case to assign them the rank of tribe.

Besides the calcar and labides termed by Pierce, hairy pads may arise from fultura inferior as in the xanthorhoinine genus *Catarhoe* Herbulot and putative *Chrysolarentia* Butler. Different build of labides in Asthenini (arising from base of the valve costa) and in Eupitheciini, Rheumapterini, Melanthiini (branching from the valve base towards the juxta and dorsally) (Figs 54, 55 and 59, 62,) is discussed above. Philereimini and some East Asiatic trichopterygines possess sclerotized arms from the base of valve costa to the anterior side of the sclerotized juxta plate.

**Female genitalia.** Female genitalia only rarely bear family-group characters and will be described accordingly below. Posterior and anterior apodemes of the female ovipositor are short or reduced (as in Xanthorhoini) when ova are laid on leaves but longer and stronger (telescopic ovipositor) if oviposition occurs in crevices.

## Tribes in Larentiinae

### Tribe *Dyspteridini* Hulst, 1896

(Figs 13–21)

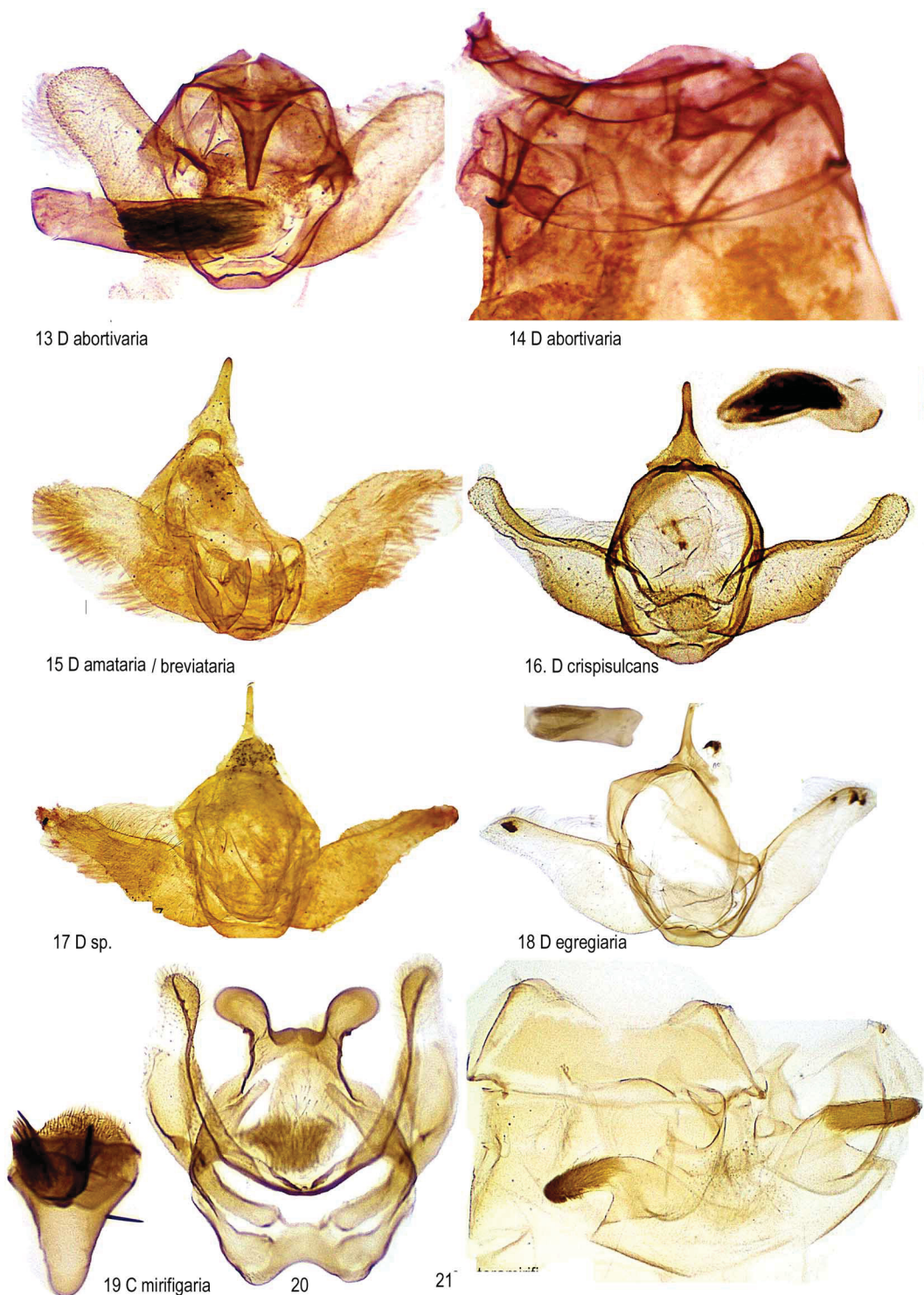
As a tribe it was separated based on characteristically modified hind wing shape and venation, different between sexes, ‘aborted’ in male, and on the presence of a small semicircular lobe at hind wing base in male, containing the remnant of a vein, supposedly An. Forbes (1917) synonymized the tribe with Hydriomenini, later (Forbes 1948)—with Lobophorini.

*Dyspteris* and *Celonoptera* share unique characters, defining here the tribe: a unique long and setose apodeme to the last abdominal segment, at tympanals (Fig. 21). As it is found, although reduced, in American species of *Dyspteris* (Fig. 14), the character distinguishes *Dyspteridini* from all the Trichopterygini;

hollow sac associated with sternite A2 in the latter tribe, is absent from *Dyspteris* and *Celonoptera*; green or white and green colour in wings; venation of wings different between sexes; a thick bundle of thin black thorns present in distal half of the dyspteridine aedeagus may well be the third apomorphy of the tribe *Dyspteridini*: vesica is sparsely or not at all ornamented in Trichopterygini. The tribe *Dyspteridini* Hulst is reinstated from synonymy with the Trichopterygini. However, male genitalia of *Celonoptera* and *Dyspteris* are very different (Figs 13 & 20). Sihvonen *et al.* (2011) show *Dyspteris* as a sister taxon to other larentiines.

**Distribution:** Neotropical and Holarctic regions (only *D. abortivaria* in Nearctic region, and only *C. mirificaria* in Mid-Mediterranean of Palearctic region).

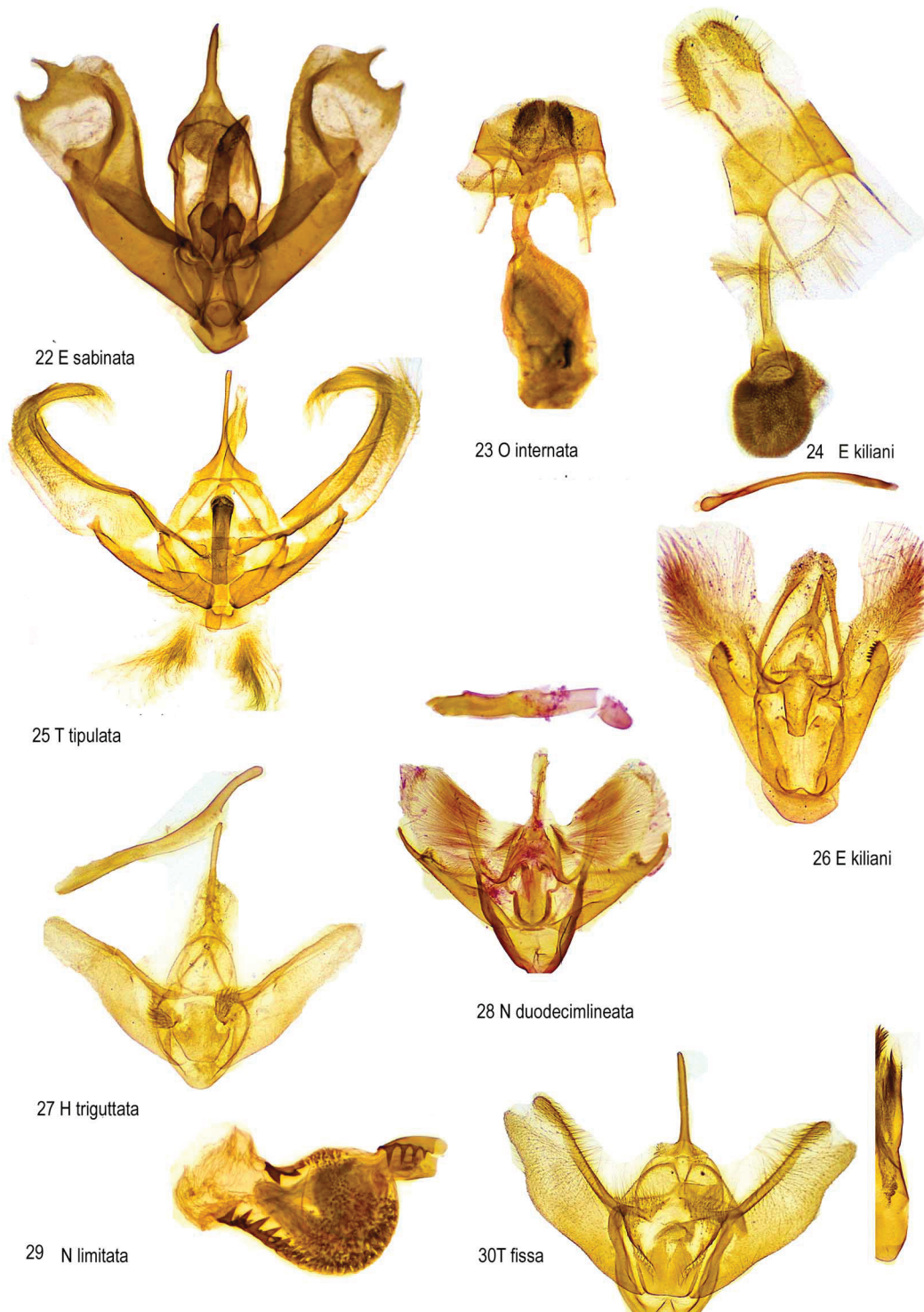




**FIGURES 13–21**, Male genitalia and anterior abdomen in Dyspteridini. 13, Male genitalia and aedeagus of *Dyspteris abortivaria* (Herrich–Schäffer) (U.S.A.); 14, anterior segments of abdomen of *D. abortivaria* (Herrich–Schäffer); 15, male genitalia of *D. breviataria* Hübner (Fr. Guiana); 16, male genitalia and aedeagus of *D. crispisulcans* Prout (Ecuador); 17, male genitalia of *Dyspteris* sp2. (Ecuador); 18, male genitalia and aedeagus of *D. egregiaria* Guenée. (Nicaragua); 19, aedeagus of *Celonoptera mirificaria* Lederer (Greece); 20, male genitalia of *C. mirificaria* Lederer; 21, anterior abdominal segments of *C. mirificaria* Lederer.

**Tribe Trichopterygini Warren, 1894**  
(Figs 22–30)

Pierce (1914) was the first to present a definition of the group (as Lobophorinae); unfortunately he also grouped two genera of the tribe Triphosini with. The genera combined now in Trichopterygini appear to be characterized by a wide ostium, and corpus bursae ornamented with petaloid signa. The variation of wing venation and sexual differences within species are markedly large.



**FIGURES 22–30.** Male and female genitalia of Trichopterygini and Asthenini. 22, male genitalia of *Epilobophora sabinata* (Geyer) (Alps); 23, female genitalia of *Oulobophora internata* (Pügler) (Turkey); 24, female genitalia of *Episauris kiliani* Rebel (Madeira); 25, male genitalia of *Tatosoma tipulata* (Walker) (New Zealand); 26, male genitalia of *Episauris kiliani* Rebel; 27, male genitalia of *Heterophleps triguttata* Herrich-Schäffer (U.S.A.); 28, male genitalia of *Nomenia duodecimlineata* Packard (USA); 29, female genitalia of *Nyctobia limitaria* (Walker) (U.S.A.); 30, male genitalia of *Triptiloides fissa* (Felder & Rogenhofer) (Chile).

The tribe is relatively well studied. Dugdale (1980) described its Australian taxa and explained the modification of male sternite A2 as a shelter for androconial pencils. Parra (e.g. 1996) studied the diversity of trichopterygine genera in Chile and Holloway (1997) that in the Indo-Australian region. Holloway (1997: 100) characterizes Trichopterygini by the reduction of the anal area of male hind wing to fold, crevice, flap or lobe(s); the 2<sup>nd</sup> sternite modified in male, having an internal, hollow sack; valva in male genitalia has both costal and saccular ornamentation; bursa copulatrix is generally scobinate (shared with Chesiadini, Eupitheciini, Melanthiini etc.), the character also occurs in Idaeini (Sterrhinae).

Trichopterygini shares the trend of modification of hind wing venation with Dyspteridini and Chesiadini. The tribe is a composite of many deeply and differently specialized elements, maintaining also archaic characters like the presence of gnathos or gnathi in some East Asiatic genera (Xue & Zhu 1999), or the occurrence of lateral appendages to juxta in a Chilean genus. Being speciose in Neotropical and Oriental faunas, only two lineages (one with the uncus conical and valva apex produced a spine, another with the uncus distal projection long and valva indented distally) have Holarctic distribution.

Dugdale (1980) and Xue *et al.* (2008) pay attention to the modification of male hind leg characteristic of this tribe: sometimes there is a thin tibial hair pencil (Fig. 73), and the trend of spur reduction has genus-level significance. However, there are at least three trends of modification, partly overlapping. Two genera, *Tatosoma* Butler, and *Tricalcaria* Han, have lost one of the medial spurs on the normally long hind legs. The *Sauris* Guenée group of genera has proximal spurs or all spurs on male hind tibia reduced and various hair tufts present (see Dugdale 1980). A thin and long hair pencil in some Holarctic genera, such as *Lobophora* Curtis, *Oulobophora* Staudinger a.o., attached to the base of male hind tibia and concealed in sternite A2 makes out the third trait (Fig. 73). The tribe is diverse and some interesting characters occur within subclades: hind wing costal venation often different between sexes; subapical thickening or clubbing of male antennae which are apically sickle-shaped; very long abdomen in male; modifications of vestiture and scaling of wings and abdomen (Fig. 72); occurrence of abdominal or valval coremata, usually concealed in the hollow structure of sternite A2, but also as hair pencils or scale tufts on male hind legs.

**Distribution:** Neotropical, Indo-Australian, Afrotropical, Holarctic. The morphological diversity of genera seems to be the greatest in South America (e.g. Parra 1996) and East Asia (Yamamoto and Sota 2007; Choi 2008).

### Tribe *Chesiadini* Pierce, 1914

(Figs 31–37)

Pierce (1914), while discussing characters of five genera, found female genitalia of *Carsia* Hübner and *Aplocera* similar to each other and substantially deviating from those of other larentiines. Forbes (1948) treated *Carsia* among the tribe Lobophorini. The names Eucestiini Warren, 1894 and Chesiadini Stephens, 1850 refer to the same concept, but Eucestiini is based on a younger synonym (*Chesias* Treitschke, 1825 = *Eucestis* Hübner, [1825]). Chesiadini Stephens, 1850 was proposed when *Chesias* was synonymized in the text to its younger synonym, *Eucestis* Hübner and therefore is not valid. Pierce (1914) was the first to use *Chesias* and Chesiadini validly.

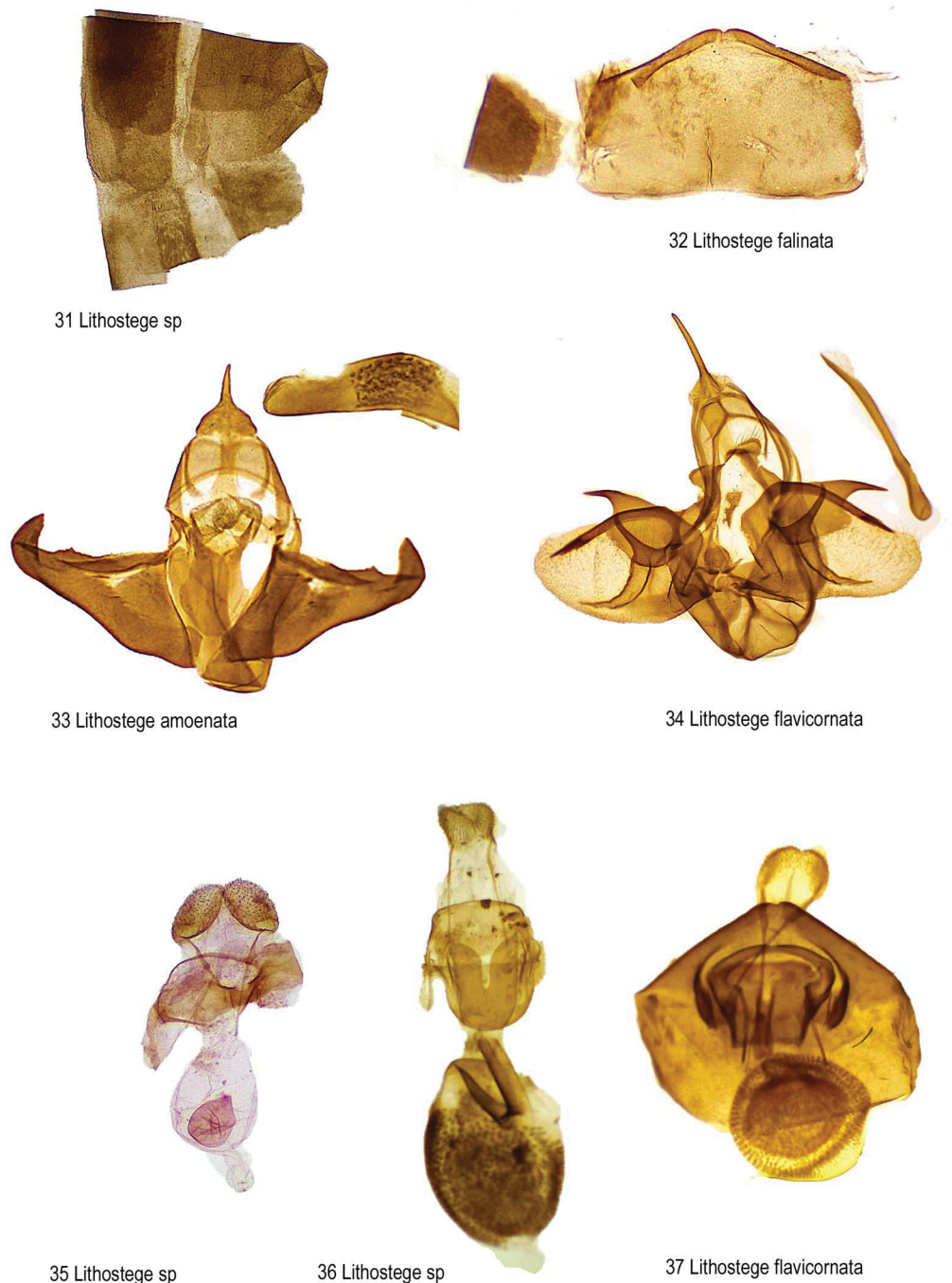
Chesiadini has apomorphic characters summarized as follows: strongly bulbed fore femora; short, flat and strong foretibia ending in two distal teeth (valid for subtribe Chesiadina, see below); remnants of gnathos fused to the posterior margin of tegumen (separate in some aplocerine genera, Fig. 47); tergite A8 rough and heavily sclerotized at its posterior margin (Chesiadina, Figs 31–32); venation of hind wing sexually dimorphic as vein An2 is absent from male but present in female; the contact of Sc with anterior margin of discal cell also varies between species and sexes (Aplocerina, see below); fringe of wings long and relatively strong; (Chesiadina) costal basal corners prolonged and produced; valval ornamentation usually medial and costal in Chesiadina, while costal, saccular and medial in Aplocetrina; bursa copulatrix generally scobinate, signa simple or petaloid (Chesiadina).

Here it is obvious that the tribe is to be divided into two groups of taxa as subtribes Chesiadina and Aplocerina, subtribe nov. (Figs 38–45). The aplocerine genera *Aplocera*, and *Carsia* possess following apomorphic characters of its own: foretibia slender with a single, external-apical dentiform projection; male genital armature large (Figs 38, 39, 40, 43), or medium sized (Figs 41, 42); valva with dorsal and saccular ornamentations present, often long (Figs 38–40); bursa copulatrix membranous, globular, without any signa (Fig. 45); ductus bursae heavily chitinized, tubular, ending in bursa in a pair of leaf-like appendages (Fig. 45); the last abdominal segment in female is completely fused into a cone (Fig. 45), while separated by thinner pleurites in Chesiadina.



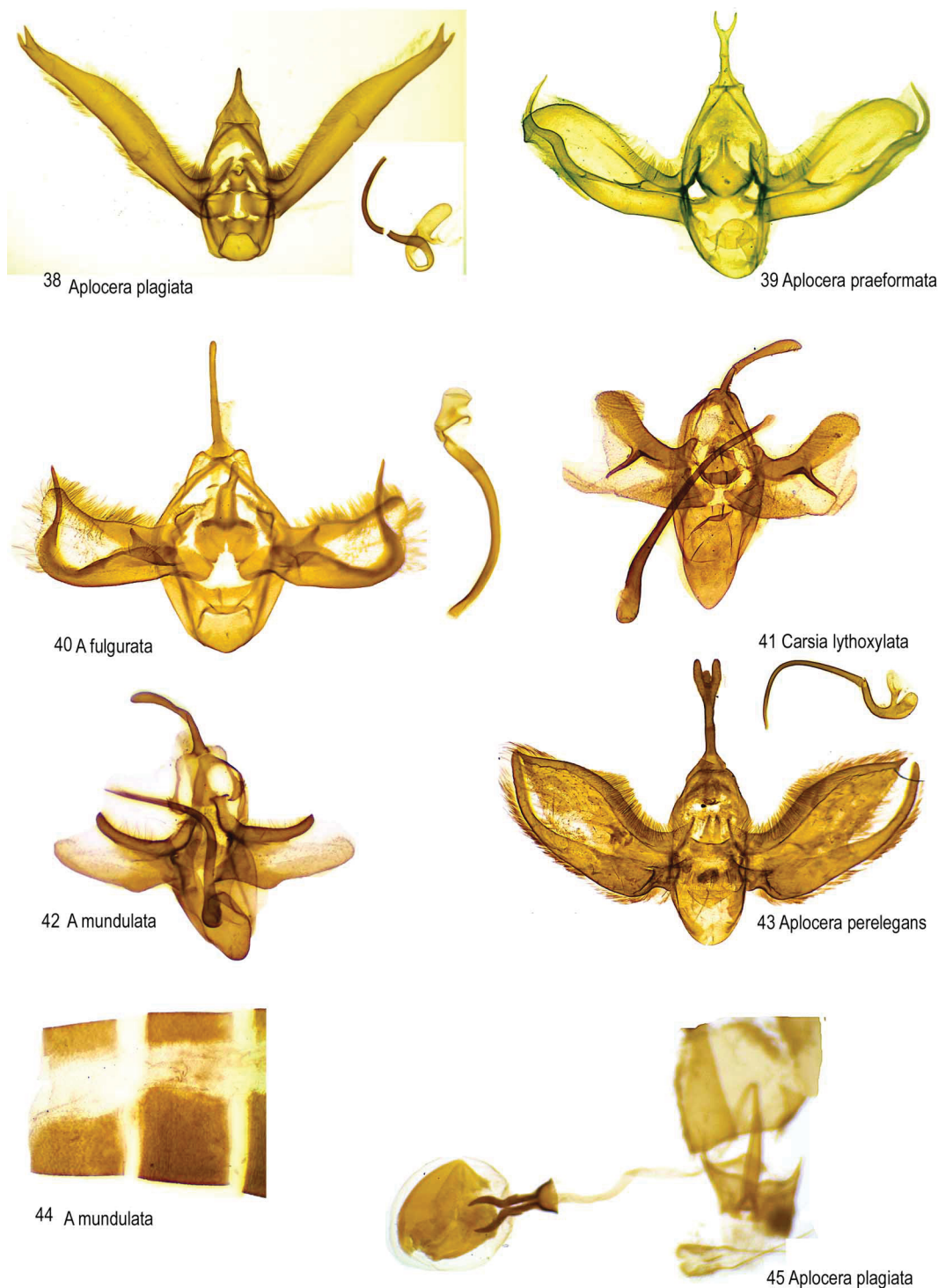
Distribution of the Chesiadina: Old-Mediterranean. Afrotropical, (Neotropical, Nearctic).

Distribution of the Aplocerina, subtribe nov. Palaearctic (penetrating as antropochorous in Australia and America).



**FIGURES 31–37**, Male and female genitalia and posterior segments of abdomen of Chesiadini. 31, Posterior abdominal segments of *Lithostege obliquata* Urbahn with a supporting buckle (Turkmenistan); 32, tergite A8 of *Lithostege farinata* (Hufnagel) with posterior margin sclerotized (Ukraine); 33, male genitalia and aedeagus of *Lithostege amoenata* Christoph (Tadjikistan); 34, male genitalia of *Lithostege flavicornata* (Zeller) (Azerbaijan); 35, female genitalia of *Lithostege turkmenica* Tsvetajev (Turkmenistan); 36, female genitalia of *Lithostege hreblayi* Rajaei & Viidalepp (Turkmenistan); 37, female genitalia of *Lithostege flavicornata* (Zeller) (Azerbaijan).





**FIGURES 38–45**, male and female genitalia of Aplocerina. 38, Male genitalia of *Aplocera plagiata* (Linnaeus); 39, male genitalia of *Aplocera praeformata* (Hübner); 40, male genitalia of *Docirava fulgurata* (Guenée) (Tibet); 41, male genitalia of *Carsia lythoxylata* (Hübner) (Armenia); 42, male genitalia of *Aplocera mundulata* (Guenée) (Armenia); 43, male genitalia of *Aplocera perelegans* (Warren) (Kunashir I); 44, last abdominal segments of *Aplocera mundulata* (Guenée); 45, female genitalia of *Aplocera plagiata* (Linnaeus).

**Tribe Eudulini Warren, 1897**  
(Figs 46, 47)

The tribe was distinguished from *Stammnodini*, by a single large accessory cell in forewing. A typical *Eudule* Hübner has thin scaling, rounded forewing, small hind wing and the abdomen extending well beyond hind wings.

Forbes (1948) characterized the tribe by: chaetosemata as a wide raised band right across the back of the head; frons rounded out and roughly scaled; eyes small and sclerite of gena broad, scaled; wings bluntly rounded, very thinly covered with scales and hairs;

Other diagnostic characters include: male genitalia characterized by the modified, large fork- or T-shaped sternite A8 (Figs 46, 47); the absence of coremata. Forewing with one accessory cell,  $R_1$  and  $R_2$  arising stalked,  $R_2$  anastomosing with  $R_3$ - $R_5$ . Valve costa with a long, jointed hook-like appendage.

Hind wing with discal vein DC straight,  $R_s$  and  $M_1$  stalked, The genus *Eudulophasia* Warren (Fig. 47) is similar to *Eudule*, differing in the costal part of the discal cell in hind wing markedly short.

**Distribution:** Neotropical, Nearctic.



46 *E. mendica*

47 *E. invaria*

**FIGURES 46–47**, male genitalia and last abdominal sternites of Eudulini. 46, *Eubaphe mendica* (Walker) (U.S.A.); 47, *Eudulophasia invaria* (Walker) (Fr. Guiana).

### Tribe *Eupitheciini* Tutt, 1896 (Figs 48–51)

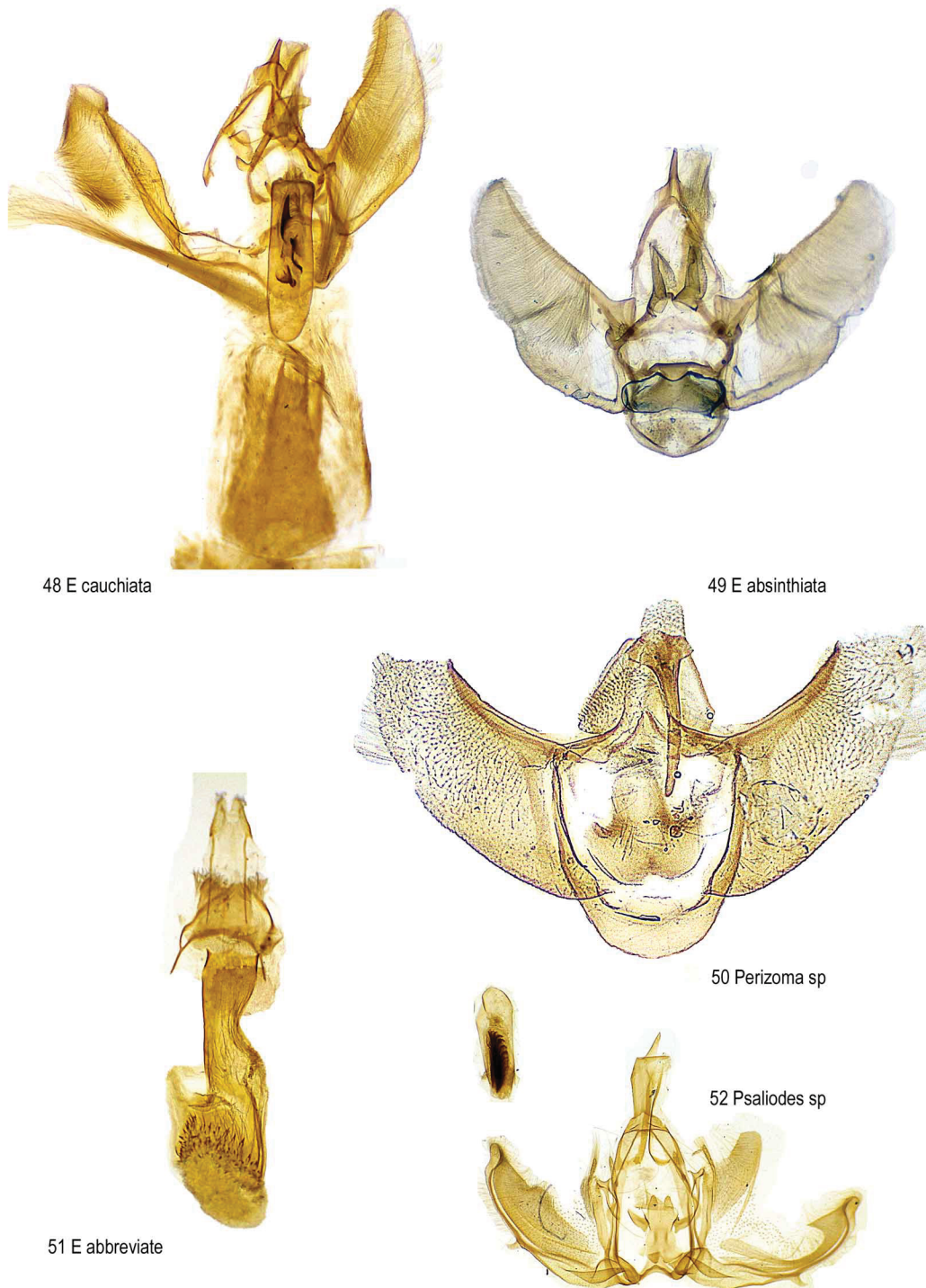
Pierce (1914: 43), in his diagnosis stresses the build of labides as diagnostic for the group: "The labides would probably form important organs for differentiation ... The papillae that occur on the feet at the labides afford to some extent a differential character in closely allied species... The juxta is a hard, rounded, chitinous plate, with two arms projecting from above".

Holloway (1997) uses the long projections from the base of valve costa anterior to transtilla furcating dorsad as labides and ventrad towards the juxta and the juxta shape to define the tribe. He refers to possible homology of this structure in Perizomini and Operophterini. A pair of coremata are present between valvae and the eighth segment, arising from cup-shaped pockets, and the specific modification of the last sternite differentiating Eupitheciini from the Perizomini, Asthenini and Operophterini.

Mironov (2003) presents an overview of morphological characters of the group distributed over all faunal regions. Small size of moths, anthophagy of larvae, and venation (one or two accessory cells in forewing, straight DC in hind wing) are not outstanding. However, the following characters are diagnostic: hourglass shape of juxta

(Figs 48, 49); species-specific modification of male sclerotized sternite A8 (Fig. 48); "labides with bifurcate setaceous papillae on their posterior arms and usually with a pair of smaller membranous and setaceous papillae on apices of their anterior ends" (Mironov 2003: 57); members of the subtribe Chloroclystina Mironov have the forewing vein  $R_1$  shortly fused to Sc, an unique feature within larentiines.

Holarctic species of Eupitheciina most often have uncus apex bifid, with short sharp dorsal and flatly rounded ventral tip; quite often the cornuti on vesica are aggregated into dentate plates, at least in *Eupithecia* Curtis; operculum and "Bolte's pockets" present in female genitalia (Mikkola, 1993); bursa copulatrix is often generally scobinate with petaloid or sternate signa (Fig. 51); larvae anto- and carpophagous on trees and herbs.



**FIGURES 48–52**, Male and female genitalia of Eupitheciini and Perizonini. 48, Male genitalia, coremata hair pencils and sternite A8 of *Eupithecia cauchiata* (Duponchel); 49, male genitalian armature of *Eupithecia absinthiata* (Clerck); 50, male genitalian armature of *Perizoma* sp.; 51, female genitalia of *Eupithecia abbreviata* Stephens; 52, male genitalia of *Psaliodes* sp. (Bolivia).



Distribution of both subtribes of Eupitheciini: all regions.

**Tribe Asthenini Warren, 1893**

(Figs 53–57)

The tribe was established (as Astheninae) by Warren (1893), characterized according to genitalia by Pierce (1914) and recently revised by Xue and Scoble (2002). Pierce described its characters as follows: valva in male with sacculus projecting long; female bursa copulatrix with a long, evenly spined signum; uncus weak and attached to dorsal side of anus tube, whereas ventral side of the tube bears a sclerotized subscaphium.



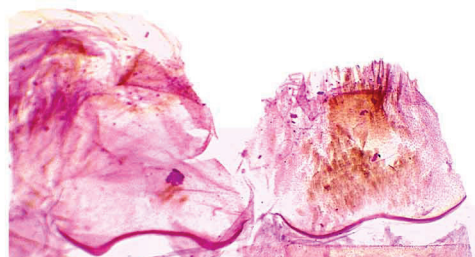
53 *L usgentaria*



54 *Poecilasthena* sp



55 *Poecilasthena* sp



54 *Poecilasthena* sp



56 *Nomenia duodecimlineata*



57 Gen. sp.

**FIGURES 53–57**, Male and female genitalia of Chesiadini and Asthenini. 53, Female genitalia of *Lithostege usgentaria* Christoph (Turkmenistan); 54, male genitalia and the last sternite and tergite of *Poecilasthena* sp. (Tasmania); 55, female genitalia of *Poecilasthena* sp. (Tasmania); 56, male genitalia of *Nomenia duodecimlineata* (U.S.A.); 57, male genitalia of “Gen. sp. 7591” (Paraguay).



Holloway (1997: 121), discussing the relations between Eupitheciini and Asthenini, noted that labides are not entirely similar in these tribes by the absence in asthenines of the branch from basal costal projection of valva towards juxta. The absence of saccular projection of valva is stressed by Pierce as another characteristic of Eupitheciini but not in Asthenini. However, Holloway grouped the relevant Indo-Australian asthenine genera to Eupitheciini according to: the presence of labides, “Springing from the points of union of the transtilla with the costa, there may arise two long arms, each bearing a soft hairy pad, and united together by a thin membrane”.

Forbes (1948) found the chaetosemata of Asthenini united by a continuous row of setae in a deep groove between scales of vertex (Figs 5, 7).

McGuffin (1958) distinguished the larvae of Asthenini as follows: the spinneret is much longer than the labial palpi; the thoracic claws are almost straight, and the angle of the notch acute.

Xue and Scoble (2002) diagnosed the asthenine as follows: uncus distal projection either absent or vestigial; uncus fused to the anal tube; the authors reject the idea of homology of asthenine and eupitheciine labides, and suppose that the build of signum in female (consisting of thin spines radiating from the central area) is the best characteristic for the tribe.

Large coremata loosely attached to the base of valva in Australian *Poecilasthena* Warren (Fig. 54) may be homologous, or not to those in Eupitheciini which are more tightly fused to valva base (Fig. 48).

There are some synapomorphies restricted to the subclades of Asthenini: frons high and broad, cylindrical, projecting; palpi short and weak (longer in *Eois* Hübner); colliculum flattened and re-folded in female at least in boreal genera; bursa copulatrix finely spiculose.

Asthenini and Chesiadini share the presence of long projections from the base of costa, which are not connected to the juxta (Fig. 56). These bear setose heads in Asthenini, but not in Chesiadini.

Distribution: Indo-Australian, Holarctic, (Afrotropical, Neotropical).

### Tribe *Melanthiini* Duponchel, 1845

(Figs 58–61)

To delimit the genera (as Melanthiinae), Pierce (1914) used characters as follows: valva well developed, complex (i.e. with projections from costal and saccular regions, rich vestiture) (Fig. 58); labides present; uncus weak, not produced; genitalia of robust form; the presence of coremata on the ninth abdominal segment; labides similar to those in Eupitheciini; large, bulbed and sclerotized ductus bursae and spined bursa (Fig. 60).

Some other apomorphic modifications of male genitalia include: juxta in male large and broad, even tending bipartite, much less chitinized than in Eupitheciini; labides arise laterally from juxta and lean against the base of costa; valva with costa concave and setose comb-like; aedeagus flattened dorsoventrally, sometimes coecum bilobed; complex ornamentation to the tip of sacculus (probably homologous with that in Rheumapterini), sometimes asymmetrical.

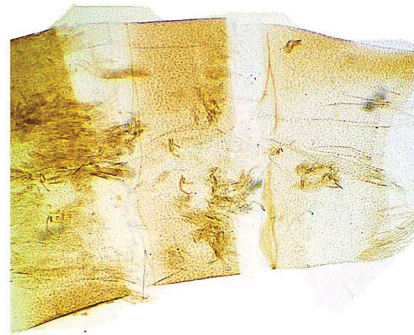
In summary, the Melanthiini differ from Eupitheciini in build of male and female genitalia, in rich ornamentation of valva, large saw-shaped dentate structures in ductus bursae, food plant association with Ranunculaceae as far as is known. *Melanthia mandshuricata* (Bremer), comb. n. is here transferred from *Mesoleuca* Hübner (Larentiini) according to its genitalia characters (Fig. 59). Holloway (1997) grouped *Collix* Guenée and *Pseudocollix* Warren with Eupitheciini (like Forbes 1948 and Ferguson 1983), arguing over the presence of long coremata between segments A6 and A7 and shorter ones between A7 and A8, associated with membranization of corresponding sternites and tergites. The described apodeme on sternite A6, the facies of the striated or pleated valva with costal ornamentation and long vestiture are somewhat curious in the context of Eupitheciini (e.g., *Eccymatoge morphna*, Fig. 61), and fit better with the Melanthiini. The shapes of signum and saw-toothed sclerite in bursa in Oriental *Collix* species fit better those in the Melanthiini.

The two African specimens studied ought to be determined as *Collix* according to the raised black scale pattern at forewing discal spot and the shape of signum in *Collix foraminata* Guenée (Fig. 60), while the male genital capsule of *Collix muscosata* Fletcher is similar to that of Palaearctic *Horisme* species up to slight asymmetry of saccular ornamentation of their valves. Pierce included *Melanthia* Duponchel, *Horisme* Hübner and *Coenocalpe* Hübner (also *Euphyia*, probably merely due to the shape of uncus) in his Melanthinae.

Distribution: Holarctic, that of *Collix* and allied forms (e.g. *Eccymatoge* Prout) Afrotropical and Indo-Australian region.



58 *C muscosata*



59 *M mandshurica*



60 *C foraminata*



61 *E morphna*

**FIGURES 58–61**, Male and female genitalia of Melanthiini. 58, Male genitalia and posterior abdominal segments of *Collix muscosata* Fletcher (Tanzania); 59, male genitalia and aedeagus of *Melanthia mandshurica* (Bremer) (Yakutia); 60, female genitalia of *Collix foraminata* Guenee (Tanzania); 61, male genitalia of *Eccymatoge morphna* Turner (Tasmania).

### Tribe *Perizomini* Herbulot, 1961

(Fig. 50)

Herbulot (1961) separated the tribe without a diagnosis. Mironov (2000, 2003) lists the characters of the tribe as follows: venation of wings characteristic in fusion of veins  $R_1$  and  $R_2$  after leaving one small accessory cell in forewing, or anastomosing also with  $R_3+R_4$  (single or double accessory cell); male genitalia with labides, "posterior arms of labides with united or bifurcate, setose papilla, anterior arms of labides sometimes with minute papillae on their apices, connected with juxta by a membrane"; uncus reduced or membranized; anterior apophyses in female usually with spurs connected with each other by a narrow, heavily sclerotized band which encircles the antrum; larvae often anto- and carpophagous.

The labides derived from, or substantially depending on the costobasal projection of valva, characterize *Perizomini*, *Asthenini*, *Phileremini*, *Rheumapterini*, *Melanthiini* and *Eupitheciini*. Two tribes, *Perizomini* and *Eupitheciini*, share a complex character of a long, setose subscaphium in anal region of male genitalia, and a doubled connection between bases of valves (transtilla and ventral projections of labides plus juxta). Labides are stemmate in both tribes, their stems being flat stripe-shaped in *Perizomini* and stick-shaped in *Eupitheciini*. The predominating anto- or carpophagy of larvae additionally supports the sistership of *Perizomini* and *Eupitheciini*.

Forbes (1948) associated a Neotropical genus *Psaliodes* Guenée with *Perizoma* Hübner. However, some putative *Psaliodes* studied from Ecuador and Bolivia lack the distinguishing characters of *Perizomini*.

Distribution: Neotropical, Afrotropical, Holarctic.

### Tribe *Rheumapterini* Herbulot, 1961

(Figs 62–63, 65–71)

Herbulot (1961) separated the tribe without a diagnosis. Large dark-coloured moths with distally dentate-edged hind wings have always been kept together in check-lists. However, there are three distinct groups of genera: the *Rheumaptera* informal group of related genera, the large-sized troglophilous species of *Triphosini*, both are treated below as tribes *Rheumapterini* and *Triphosini*, respectively. The third, *Phileremini* consists of a few Palearctic species with several specific traits as listed below.

The tribe *Rheumapterini* shows a long list of apomorphic characters: juxta dorsal part rooted in the basal part of it (Figs 62–65); a slender sclerite present between juxta, saccus and bases of sacculi (Fig. 62). It is not clear whether this sclerite is analogous to that in *Cataclymini*; The *rheumapterine* genera are characterized here by: wide posterior sclerotisation of female genitalia (possibly shared with *Melanthiini*?) (Figs 66–68); uncus heavily sclerotized, broad, flat, triangular, trapezoidal or cupola-shaped (skinny soft and hairy in *Melanthiini*); both costal and saccular ornamentations of valva present (like also in *Melanthiini*); labides arise from the base of costa, are connected by a membrane, supported by a median sclerite, long, headed, reaching uncus (Figs 62–65); dorsal parts of vinculum flattened and invaginated into bases of valvae; presence of coremata associated with membranization of the eighth abdominal segment in male and large masses of deciduous hair-scales (Fig. 71).

Some apomorphic characters of subclades occur within the tribe, such as: shortening of spurs on male hind tibia; rich vestiture of male hind tibia associated with shortened and thickened tibia, and the basal tarsomere (Figs 69, 70); the presence of blotches of specialized scales in wings of male; posterior sclerotization of female genitalia; fusion of cornuti in male aedeagus and signa in female bursa copulatrix into conglomerates.

**Distribution:** Neotropical, Holarctic.

### Tribe *Triphosini* Tutt, 1896

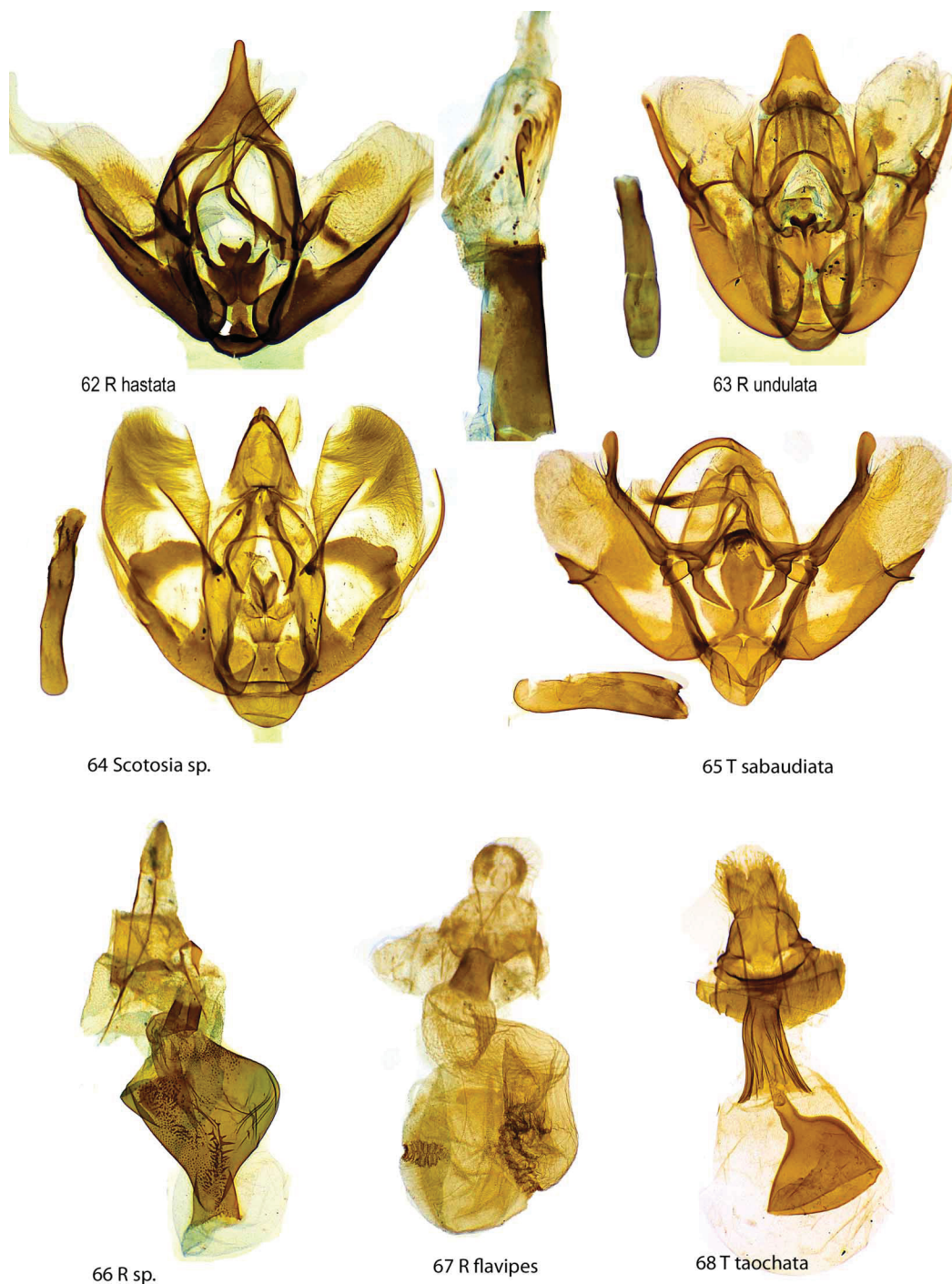
(Figs 65, 68)

I have not found the original description of this tribe by Tutt. Herbulot (1961) grouped both *Triphosa* Stephens and *Philereme* Hübner with *Rheumapterini*. However, Viidalepp (2006) found characters to distinguish between *Triphosini* and *Rheumapterini* (Fig. 155): modification of wing coupling structures in male (*Strepsizuga* Warren); uncus long, strong, hooked finger-shaped; valve costa specifically modified, projecting roundish (Fig. 65); costal



projection just opposite the saccular projection; short labides at costobasal corners of valve; juxta dorsal part is large, its dorsum edged smooth, not indented heart-shaped; costa sclerotized, costal and saccular processes short (as in *Pareulype* Herbulot); signum is a smooth plate.

Distribution: Neotropical, Holarctic.



**FIGURES 62–68**, Male and female genitalia of Rheumapterini and Triphosini. 62, Male genitalia of *Rheumaptera hastata* (Linnaeus); 63, male genitalia of *Hydria undulata* (Linnaeus); 64, male genitalia of “*Scotosia*” sp. (Nicaragua); 65, male genitalia of *Triphosa sabaudiata* (Duponchel) (Crimea); 66, female genitalia of *Rheumaptera hyrcana* (Staudinger) (Turkmenistan); 67, female genitalia of *Rheumaptera flavipes* (Menetriès) (Kunashir I.); 68, female genitalia of *Triphosa taochata* Lederer (Iran).





69 *C meadi*

70 *R hyrcana*



71 *R hyrcana*



72 *T tipulata*



73 *O internata*

**FIGURES 69–73**, Vestiture of legs and abdomen in Rheumapterini and Trichopterygini. 69, Male hind tibia of *Coryphista meadi* Packard (U.S.A.); 70, male hind tibia of *Rheumaptera hyrcana* Staudinger (Georgia); 71, membranized abdominal segment A8 in *R. hyrcana* Staudinger (Georgia); 72, body ventral side vestiture of *Tatosoma tipulata* (Walker) (New Zealand); 73, male hind leg with hair pencil of *Oulobophora internata* (Püngeler) (Turkey).

### Tribe *Phileremini* Pierce, 1914

(Fig. 74)

The tribe was based on two characters, one of these very characteristic: very large valva associated with a tiny tegumen; which can be complemented as follows: labides from base of costa (but with tips united to juxta in *Philereme transversata*); uncus needle-shaped, long and thin; subscaphium very long; valva inner side vestiture fine and dense; small aedeagus with tiny cornuti; emale genitalia membranous, ostium with cingulum, ovipositor telescopic.

The small labides and the doubled connections from base of valve costa to juxta delimit the tribe with respect to Rheumapterini. Foodplant association with Rhamnaceae, larvae spin leaves on shoots in a “cigar” like those of Rheumapterini: a possible synapomorphy.

Distribution: Palearctic.



**FIGURE 74**, Male and female genitalia of *Philereme transversata* (Hufnagel) (Phileremini).

### **Tribe *Operophterini* Packard, 1896**

(Figs 75–77)

Forbes (1948) described the tribe as follows: a pair of small sclerites lateral to clypeus present and naked gena as autapomorphies of the tribe; long accessory cell in forewing and peculiarities of venation and phenology; micropterism of females, associated with high fecundity. Some East Palearctic species of *Operophtera* Hübner and related genera with fully winged females share the above characters with *Epirrita* Hübner.

The group of “winter moths” has been discussed from the aspects of its extreme traits of bioecology and female micropterism. Yamamoto and Sota (2007) and Snäll *et al.* (2007) have also tried to elucidate the position of Operophterini within the subfamily and the timing of its speciation. Snäll *et al.* (2007) found sister-group relationships between Perizomini and Operophterini; from the aspect of comparative morphology, both share long labides which fuse together at the apex. Operophterin has a stout uncus and Epirrita - specifically modified male sternite A8 (Figs 75, 76)

The following traits characterize the tribe supplementally: ecological trait: polyphagous on trees and shrubs; male antenna ciliated long (shared with Alsophilinae and some ennomine winter moths); labides arise from juxta, while the connection to costa base is membranous (shared with Melanthiini); labides tips united roof-like upon the juxta.

The tribe is restricted to the Holarctic region, being most speciose in East Asia.



**FIGURES 75–77**, Male genitalia of Operophterini. 75, Male genitalia, aedeagus and sternite A8 (“octavals”) of *Epirrita dilutata* (Denis & Schiffermüller); 76, male sternite A8 of *E. christyi* Allen; 77, male genitalia of *Operophtera relegata* Prout (Primorye).

### Tribe *Erateinini* Guenée, 1858

(Figs 84–88)

*Erateina* Doubleday, 1848 has been paid little attention since it was raised to subfamily rank by Guenée (1858). Forbes (1917) characterized the genus by the absence of a frenulum (in both sexes), bent discocellulars in both wings, the anal area of hind wing lobed and folded down in *Erateina* and less modified in *Trochiodes* Cuenée, sexual differences in wing shape.

Erateinine moths are day-active, resting in veliform position. Male genitalia of *Erateina punsaria* Guenée, studied have a cidariine genital capsule with the uncus finger-shaped, tegumen more slender than the vinculum, valva with large costa bordered against valvula by lacinia costalis, and a slightly projecting sacculus (Fig. 88). The juxta is broad between bases of sacculi, there are sclerotized connections between juxta and hemitransstilla and short membranous papillae at base of hemitransstilla. Female genitalia are characteristically small sized with ostium sclerotized, ring-shaped, apophyses long and ovipositor papillae conical and strong (Fig. 87). *Erateina* as described by Doubleday is composite, its sections obviously representing different genera (Figs 84–88).

Distribution: Neotropical, (Nearctic).

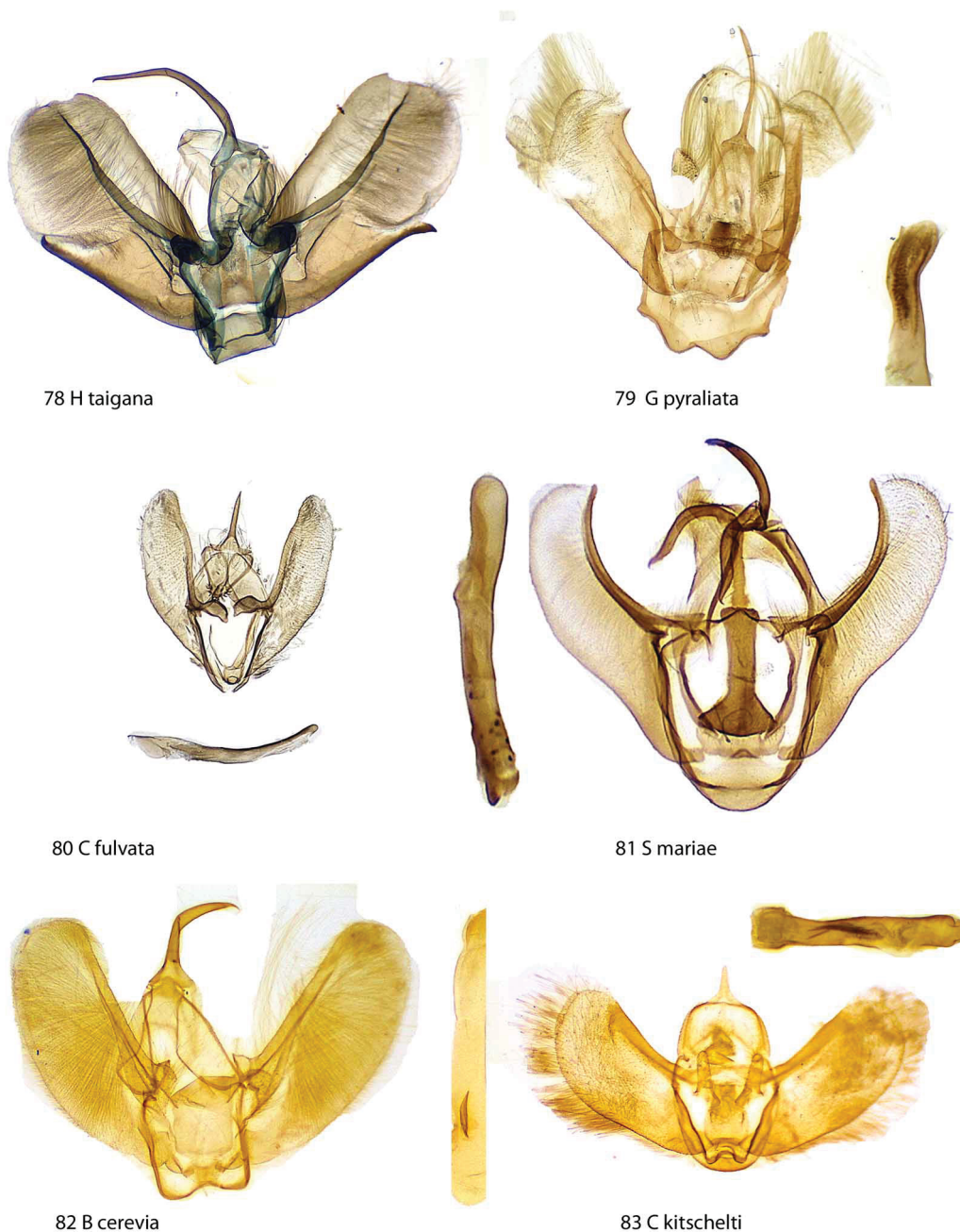
### Tribe *Cidariini* Duponchel, 1845

(Figs 78–80, 82–83)

Pierce (1914) discussed the genera, now placed in the tribes Cidariini and Hydriomenini, together, listing the common characters as follows: “a rather compact group, composed of a few closely allied genera. The large simple valva, and the extended anellus lobes. Often with clavate scales, ... manica finely spined. The signum ... small, scobinate”. However, concerning the first included genus, *Lampropteryx* Stephens, it is added that there is a “hinge” between the ninth and the tenth segments (i.e. between tegumen and uncus), and Pierce described the labides attached to the point of connection of transtilla and tegumen. Labides of *Lampropteryx* Stephens and *Nebula* Bruand have labides bipartite, with a hinge between.

Pierce separated the subfamily Therinae for the species with “costa well developed, sacculus extended, aedeagus ctenoid at orifice and anellus lobes strong, with spatulate scales.” Forbes (1948) has collected an over-heterogeneous assemblage of genera under his equivalent of Cidariini (Hydriomenini).





**FIGURES 78–83.** Male genitalia of Cidariini and Solitaneini. 78, Male genitalia and aedeagus of *Pennithera taigana* (Djakonov) (Primorye); 79, male genitalia and aedeagus of *Gandaritis pyraliata* (Denis & Schiffermüller); 80, male genitalia and aedeagus of *Cidaria fulvata* (Forster); 81, male genitalia and aedeagus of *Solitanea mariae* (Stauder) (Italy); 82, male genitalia and aedeagus of *Brabirodes cerevia* Druce (Nicaragua); 83, male genitalia and aedeagus of *Colostygia kitschelti* (Rebel) (Switzerland).

Choi (e.g. 1997), Viidalepp and Kostjuk (2005) and Viidalepp (2003) have analyzed different sets of cidariine genera using cladistic methodology. Choi (1997) found seven strict synapomorphic characters to support the monophyly of the tribe: bulged postmedial line of the forewing; long male eighth abdominal segment; oblong or posteriorly broad male eighth sternite; absence of calcar; membranous female eighth tergite; ostium with sclerotized short cingulum, which is open dorsally; SV4 seta of larval third abdominal segment outside the L1–SV1 line; moderate and rounded paraprocts in larva.

Choi (2007) found four characters discriminating *Thera* Stephens: valve costa with medial projection; cucullus large; cornuti, a few in number, arranged corona-like around the aedeagus mouth.

He paid attention to characters of anellus and relations of tegumen and vinculum in male genitalia, and synonymized Therini Pierce with Cidariini, Viidalepp and Kostjuk (2005) analyzed a case of character reduction on the



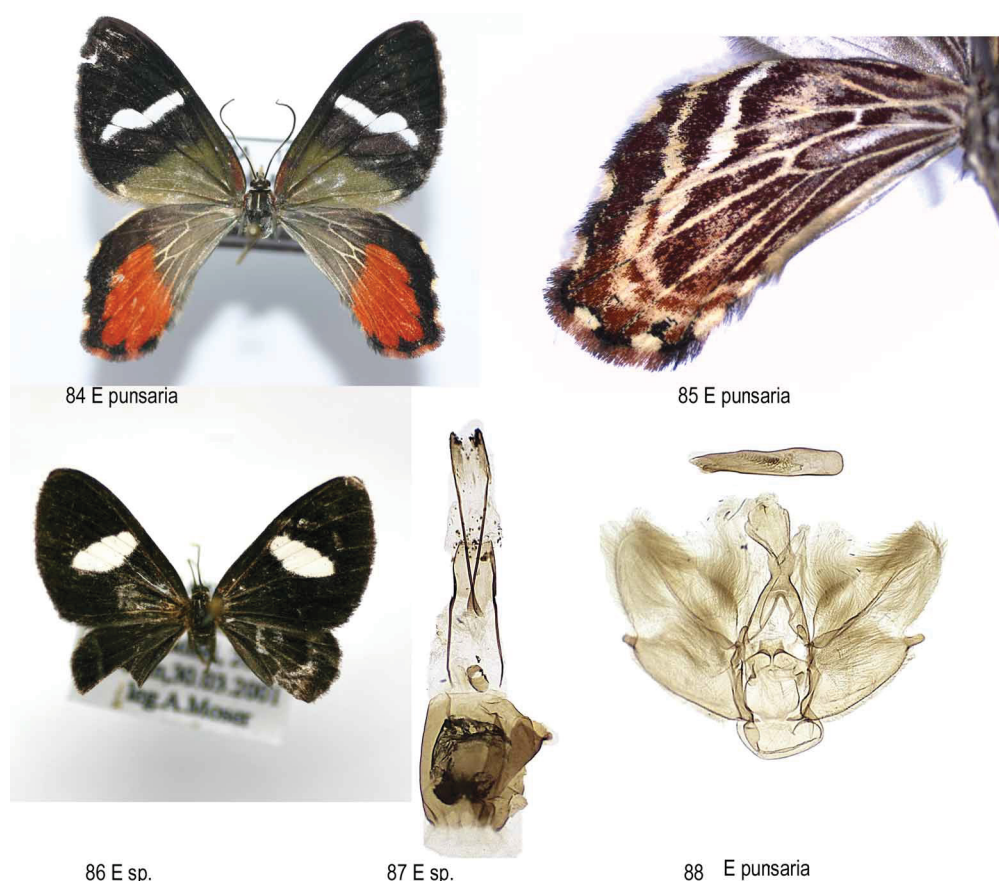
cidariine background. Retrograde evolution of morphological characters, if occurs, then in several sections of a group, and will be ignored by cladistic methodology. Another case study of the Mediterranean genus *Protothera* (Viidalepp 2003) demonstrated how essential it is to include more than one representative species of each group into a matrix for cladistic analysis to be sure that their synapomorphic traits will be revealed. These studies revealed the presence of four main clades within Holarctic Cidariini, characterized by synapomorphic traits: conifer-feeding genera with male genital capsule well sclerotized and valva a plate „with sacculus tip projecting sclerotized” (*Thera* Stephens and allies); presence of specialized thick setae (hamuli) on labides (*Nebula* Bruand and allies); valva with a subcostal furrow on inner side, between costa and valvula, associated with vestiture on medial wall of valva long and springing from ring-like ornamentation; thick vestiture to labides, consisting of clavate hairscales, associated with long palpi in moths.

The variation of putative cidariine genera in Neotropical fauna (e.g. *Brabiroides cerevia* Druce, Fig. 82) is considerably larger than in boreal fauna.

Scarce data on *Erateina* indicate a kind of similarity to Cidariini (see also discussion under Eratenini). The genus *Hagnagora* Druce has some similarities to Cidariini as well:

However, Sihvonen *et al.* (2011) showed *Hagnagora* clustered with *Hydriomena*. This may be correct as *H. vittata* Philippi has more setae on proleg of mature larva than typical to cidariine larvae studied (King & Parra 2011; Viidalepp 2006). *Hagnagora clustimena* Druce (Figs 149, 150) has a solid male genital armature with putative clusters of androconian hairscales at uncus base and bases of valvae. *H. ephestris* Felder and Rogenhofer (Figs 151, 152) has a pyriform bursa with well defined cingulum and with two longitudinal bands of flat signa. King & Parra (2011) described the biology and larval characters of *Hagnagora vittata* Philippi.

Distribution: Neotropical, Holarctic.



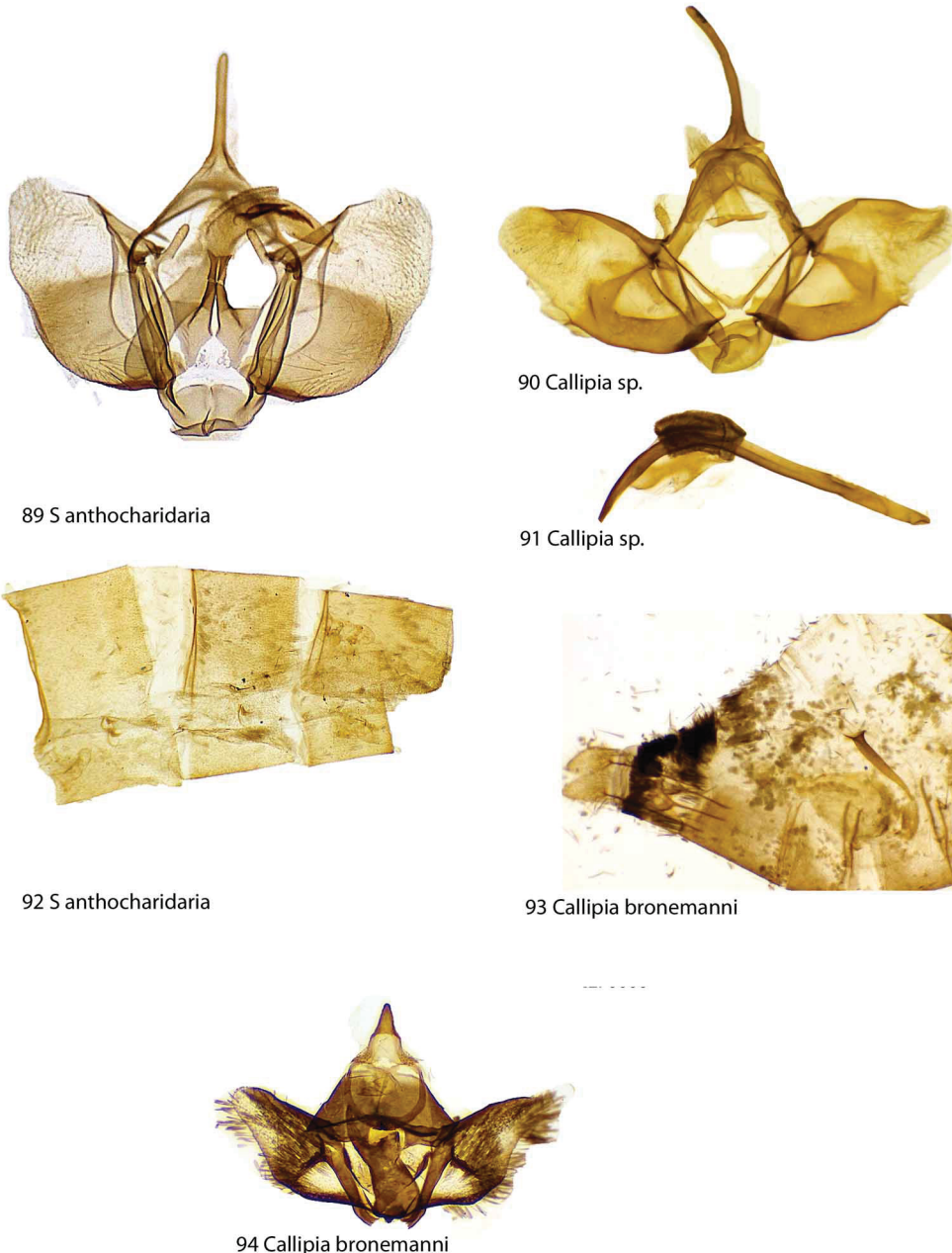
**FIGURES 84–88**, Wings, male and female genitalia of Erateinini. 84, Male *Erateina punsaria* Dognin (Ecuador); 85, male hind wing of *E. punsaria* Dognin from underside; 86, female *Erateina* sp. (Brazil); 87, female genitalia of *Erateina* sp. (Brazil); 88, male genitalia of *E. punsaria* Dognin (Bolivia).

### Tribe *Stamnodini* Forbes, 1948

(Figs 5, 6, 89–93)

Forbes (1948) characterized the genera *Stamnodes* and *Heterusia* by: veliform resting position (wings folded butterfly-like on back, resulting in plain pattern above and contrasting markings in wings' underneath). Moths are active in the sun and dusk (Mikkola *et al.* 1987).

These characters are to be complemented as follows: juxta is shield-shaped with specific ornamentation; sclerotized connections from juxta to short hemitransstilla present; subscaphium arising bifurcate from tegumen (a putative homology with Euphyiini) and distally anchor-shaped or consistent with Neotropical *Stamnodes* and *Callipia*; valva with a strong costal hair lock; valva rounded with costa and sacculus wholly fused to.



**FIGURES 89–93**, Male and female genitalia and abdominal sclerites of Stamnodini. 89, Male genitalia of *Stamnodes anthocharidaria* Oberthür (Ecuador); 90, male genitalia of *Callipia* sp. (Bolivia); 91, aedeagus with manica and fultura inferior of *Callipia* sp. (Bolivia); 92, posterior abdominal segments of *S. anthocharidaria* Oberthür (Ecuador); 93, posterior abdominal segments of female *Callipia brenemanni* Sperry (Bolivia); 94, male genitalia of *Callipia brenemanni* Sperry (Bolivia).

Ferguson (1983) grouped *Heterusia* with *Stamnodes* as suggested by Forbes (1917). Both have thick tufts of clavate hairscales to valval costa, the shape of scaphium, position of the juxta within the genital capsule and its sclerotized connections to hemitransstilla are common, according to scarce material studied. Hausmann (2007) lists Heterusiini as a tribe.

Distribution: Neotropical, Nearctic, (Palearctic).

### Tribe *Solitaneini* Leraut, 1980

(Fig. 81)

Leraut (1980) separated the tribe without giving a diagnosis. The genus *Solitsnea* Djakonov has some unusual for larentiines features: female bursa copulatrix with a ring of flat spines across the equatorial part; tegumen with a pair of tapering projections with unknown function; valva with all its parts well fused and chitinized, flat, without ornamentation.

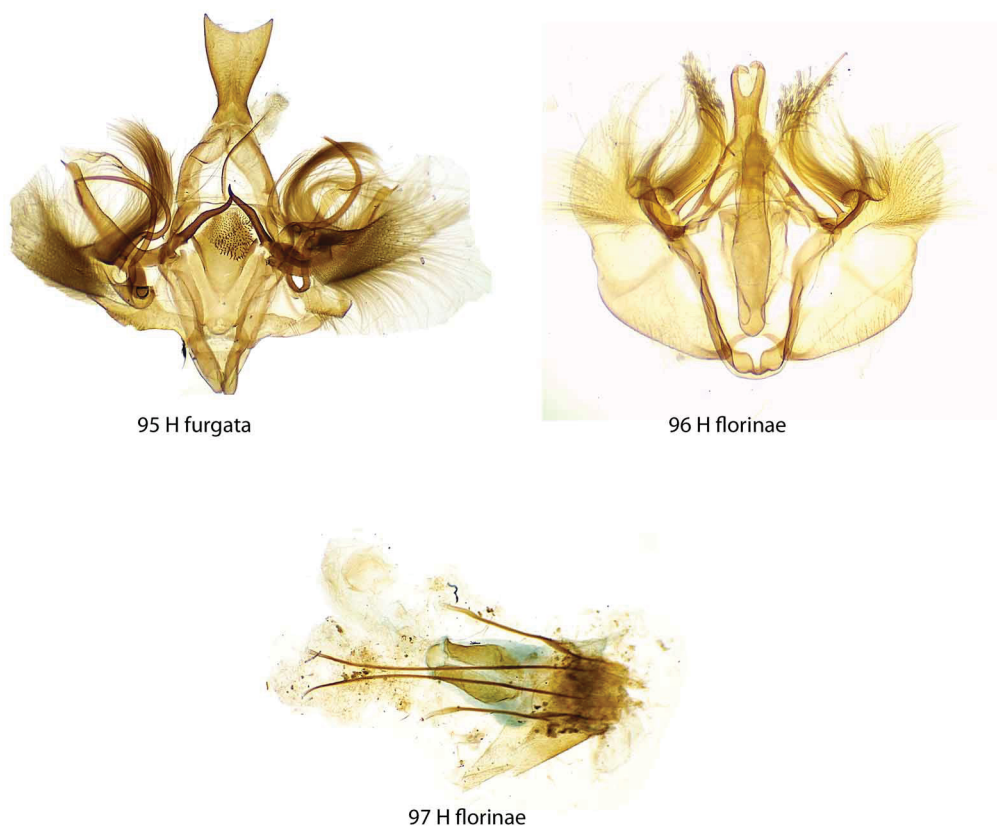
It is noteworthy that flat signa occur in female bursa of the Erateini too, but arranged into a longitudinal band. Sihvonen *et al.* (2011) included the Solitaneini in their tree but used *Baptria* Hübner as an example species; however, *Baptria* is just an as solitary genus in Larentiinae as *Solitanea* is.

Distribution: Palearctic.

### Tribe *Hydriomenini* Meyrick, 1872

(Figs 95–97)

The tribe is discussed here as delimited by Herbulot (1962). The tribe is composite in the treatment by Forbes (1948), and Ferguson (1983) when characterized as: front sloped and tufted or thickly scaled below; metathorax strongly tufted; the upper discocellular bent in hind wing and  $M_2$  closer to  $M_3$  than  $M_1$ .



**FIGURES 95–97**, Male and female genitalia of Hydriomenini. 95, Male genitalia of *Hydriomena fuscata* (Thunberg); 96, male genitalia of *Hydriomena furinae* Schaus (Costa Rica); 97, female genitalia of *H. furinae* Schaus (Costa Rica).



Herbulot (1961-1963) moved *Mesoleuca* Hübner and *Entephria* Stephens from Hydriomenini s. l. to Larentiini, other genera to Cidariini, Perizomini and Rheumapterini and restricted Hydriomenini for the nominate genus. McDunnough (1954), dealing with Nearctic species of the genus *Hydriomena* Hübner listed its characters as follows: specific shape of uncus, flat, bifurcate or dilated apically; modifications on costal region of valva (tubercles, bearing single stiff, curved seta („ribbon”) and locks of specialized hairscales); large, sparsely setose plate of juxta with dorsoapical papillae in male; membranous bursa copulatrix almost without signa but with heavily sclerotized ductus bursae, and semiglobular chitinous digitabulum attached to the latter in female; hemitransstilla connections to juxta membranous; manica rugose, not spiny.

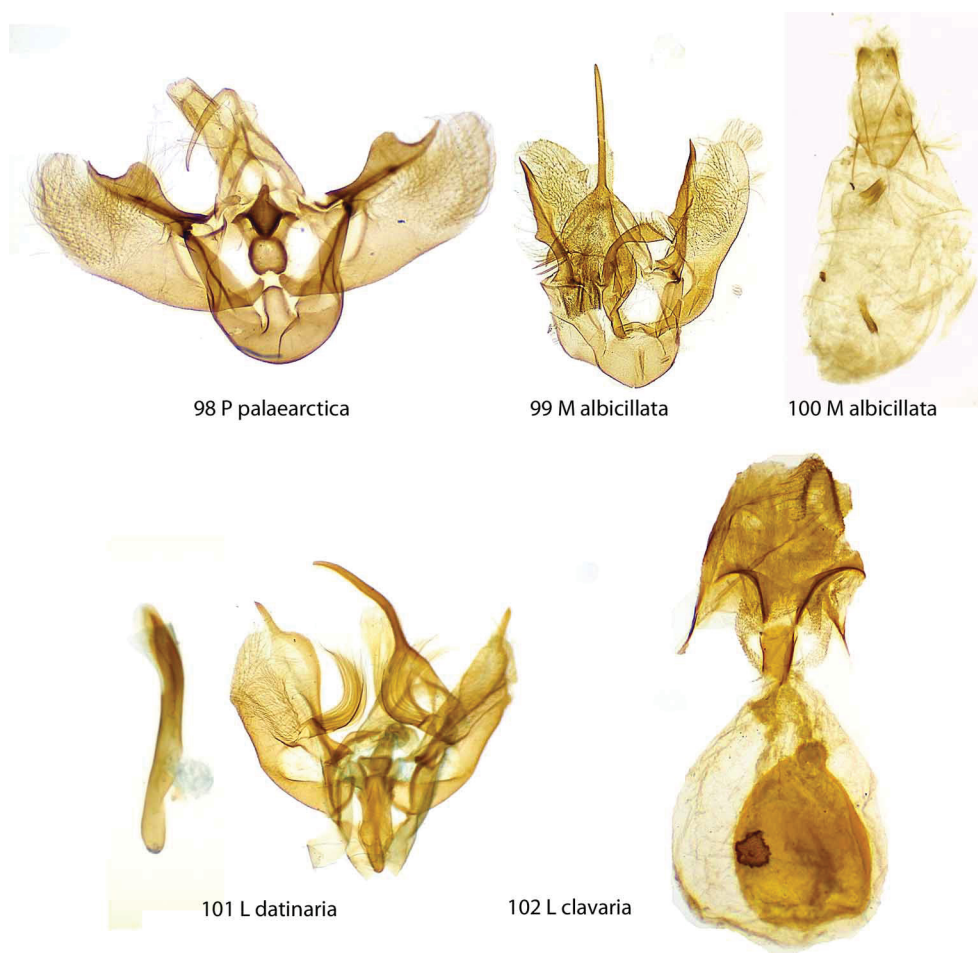
The presence of a long costal or subcostal hair lock is shared, although less complicated, by Larentiini, Stamnodini and some Neotropical genera not assigned to tribes. The digitabulum to the female bursa seems to be characteristic to the species from the northern hemispheric (Figs in McDunnough 1954).

Distribution: Neotropical, Nearctic, (Palearctic).

### Tribe *Larentiini* Duponchel, 1845

(Figs 98–107) (Mesoleucini McGuffin, 1958)

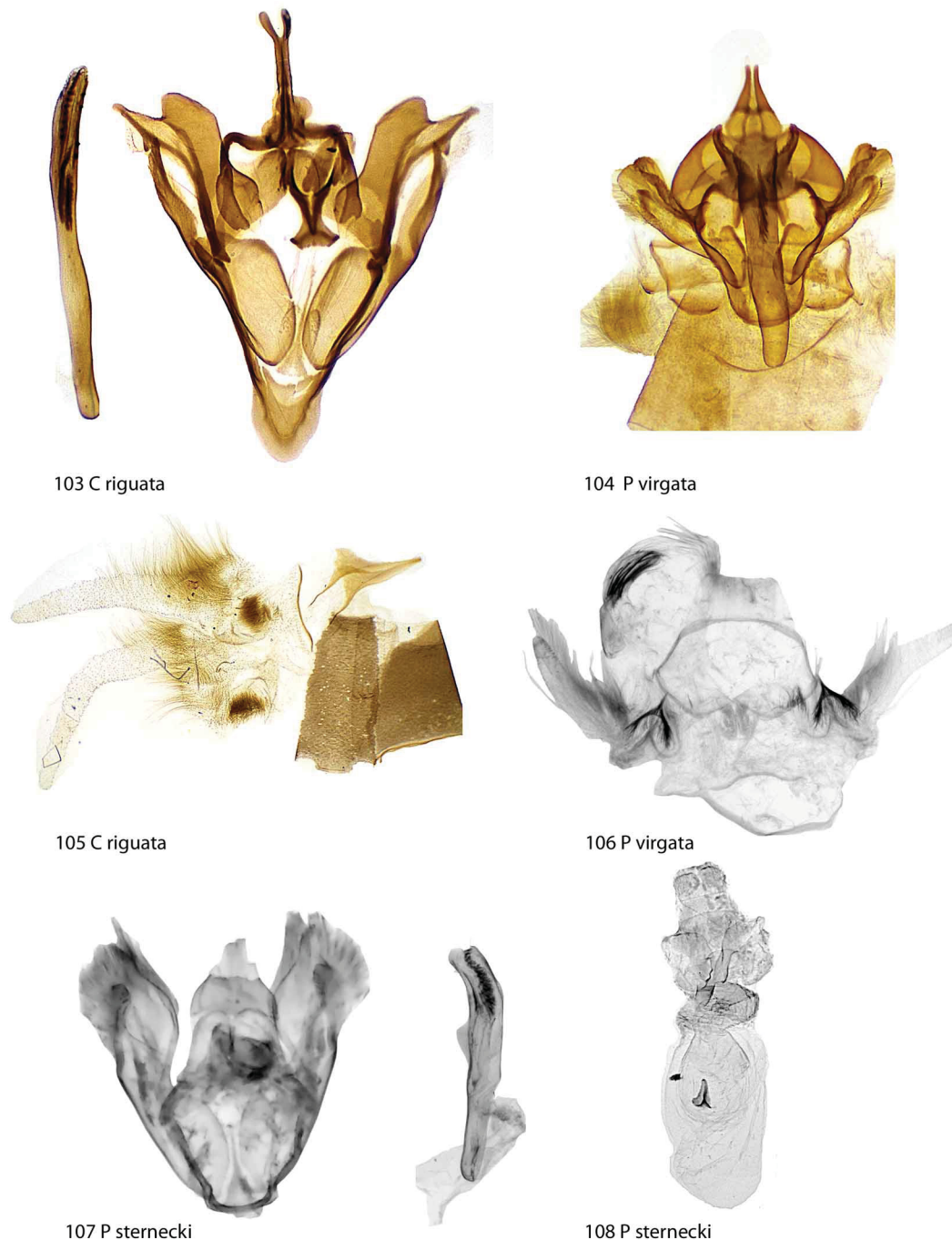
Pierce (1914) described his group “Entephriinae” as follows: valva rounded (i.e. sacculus region wholly fused to), costa thickened, plate-like; manica thickly and minutely spined; anellus dorsal lobes or calcar [present]. (Pierce grouped some *Colostygia* Hübner (Fig. 83) species with *Entephria*, therefore anellus lobes mentioned); calcar produced to a long arm is mentioned in texts for *Entephria* Stephens species; medially dilated valve costa reminds that in *Thera* Stephens and allied cidariine genera but differs in pollex -like outstanding apical process.



**FIGURES 98–102**, Male and female genitalia of Larentiini. 98, Male genitalia of *Photoscotia palaeartica* (Staudinger) (Kyrgyzstan); 99, male genitalia of *Mesoleuca albicillata* (Linnaeus); 100, female genitalia of *M. albicillata* (Linnaeus); 101, male genitalia of *Larentia datinaria* (Oberthür) (Malta); 102, female genitalia of *Larentia clavaria* (Haworth).

Following characters enable us to delimit the tribe: male genital armature with dorsal arms of vinculum dilated triangular, tegumen much slender; a thick hair lock arising from base of valve costa; female apophyses short (shared with Xanthorhoini); vinculum projecting flap-like between the bases of sacculi.

McGuffin (1958) separated a tribe Mesoleucini from Hydriomenini s. l. according to morphological characters of larvae; Herbulot recombined these genera into Larentiini. Krüger (2005) has described some species of *Entephria* with *Piercia*-like ornamentation to juxta. Distribution: (Neotropical, Afrotropical), Palaearctic.



**FIGURES 103–108**, Male coremata, male and female genitalia of Cataclymini. 103, Male genitalia and aedeagus of *Cataclysmes riguata* (Hübner) (Marocco); 104, male genitalia and posterior segments of abdomen of *Phibalapteryx virgata* (Hufnagel); 105, coremata of male *C. riguata* (Hübner) (Marocco); 106, the last abdominal segments and coremata of *P. virgata* (Hufnagel); 107, male genitalia and aedeagus of *Paraplaneta sternecki* (Prout) (China); 108, female genitalia of *P. sternecki* (Prout) (China).



109 P prasinaria



110 P prasinaria



111 K marginata



112 K marginata

**FIGURES 109–112**, Male genitalia of the genera *Piercia* Prout and *Kauria* Viidalepp. 109, Male genital armature of *Piercia prasinaria* (Warren) (South Africa); 110, female genitalia of *P. prasinaria* (Warren) (South Africa); 111, male genitalia of *Kauria marginata* Viidalepp (Tadjikistan); 112, posterior abdominal segments of male *K. marginata* Viidalepp (Tadjikistan).

### Tribe *Scotopterygini* Warren, 1895 (=Ortholithinae Pierce, 1914)

(Figs 113–116)

Prout (1912) distinguished the genus *Ortholitha* according to its hind wings longer than anal margin of forewing. Pierce (1914) (as Ortholithinae, following Xanthorhoinae) found numerous differences to the former besides coremata present at eighth abdominal segment; Choi (2006) published the results of a cladistic analysis of Xanthorhoini sensu Holloway, i.e. coremata-bearing genera where six *Scotopteryx* species appeared as placed in a lineage sister to Xanthorhoini and several other tribes. In analyses by the author, the species of this genus also group out at their own subclade due to some peculiar characters: valva very complex, with all its parts sclerotized; with costa a broad plate; uncus weak; uncus with raised hairy pads (putative remnants of socii) at base; canaliculus as a sclerite, fused to juxta and aedeagus; coremata the shortest in the tribe, associated with the eighth, dissclerotized segment.

African species grouped with *Scotopteryx* by Janse (1932-1935) have somewhat different genitalia.

Distribution: Palaearctic (Afrotropical?).





113 *S. chenopodiata*



114 *S. chenopodiata*



115 *S. kuznetzovi*



116 *S. bipunctaria*

**FIGURES 113–116**, Male genitalia and coremata of Scotopterygini. 113, Aedeagus and male genitalia of *Scotopteryx chenopodiata* (Linnaeus); 114, abdominal segment A8 and coremata of *S. chenopodiata* (Linnaeus); 115, male genitalia of *S. kuznetzovi* Wardikjan (Armenia); 116, male genitalia of *S. bipunctaria* (Denis & Schiffermüller) (?) (South Ural).

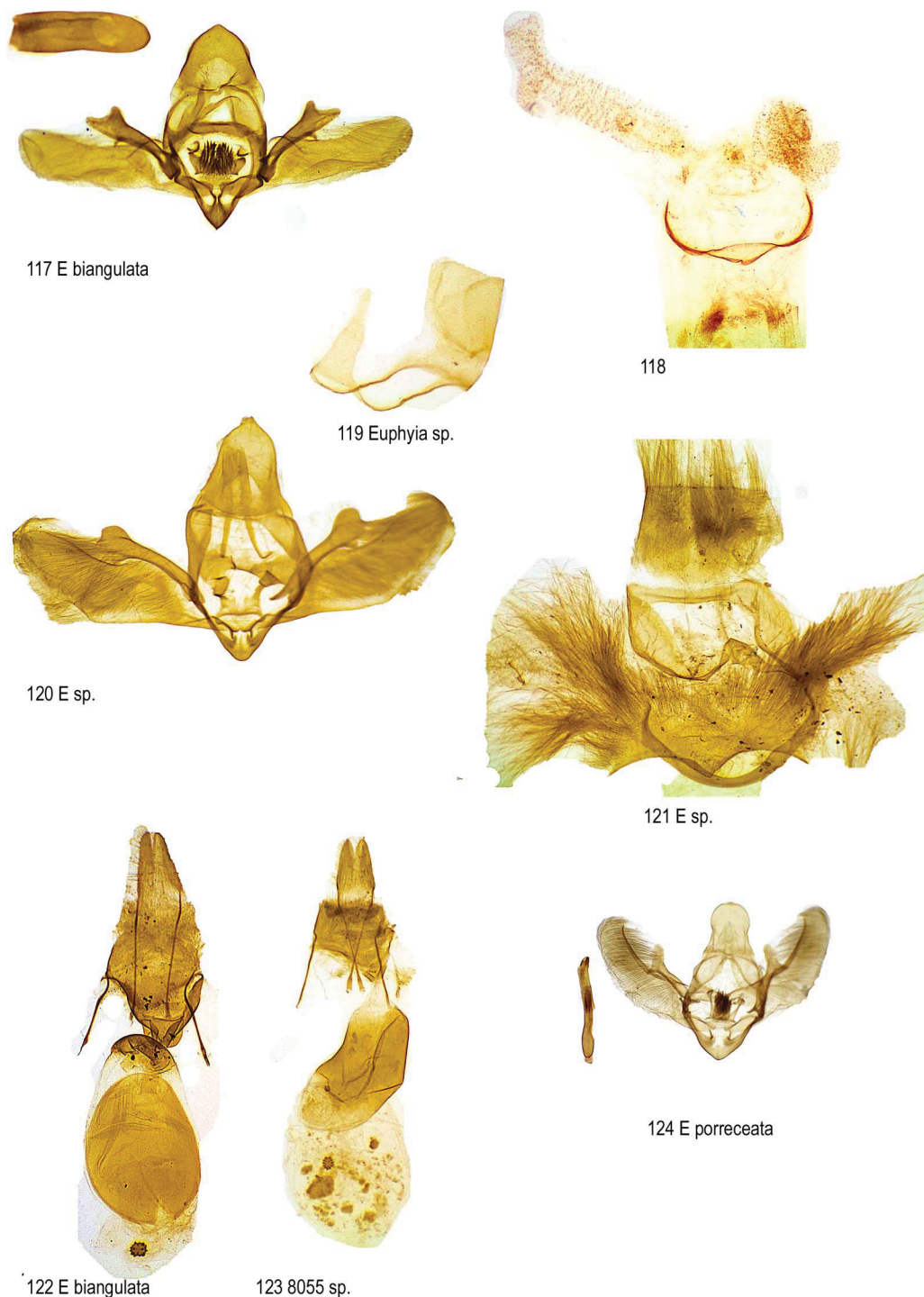
### Tribe *Euphyiini* Herbulot, 1961

(Figs 117–123)

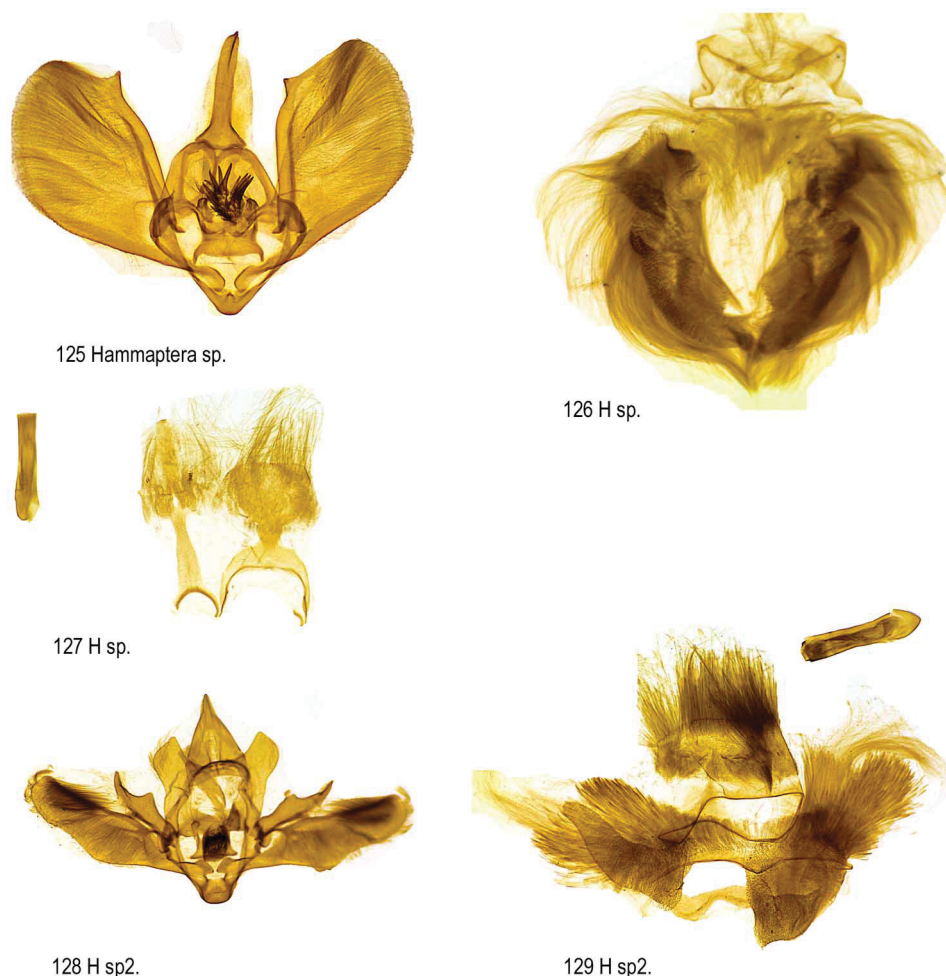
Herbulot (1961) separated the tribe without a diagnose. *Euphyiini* may be distinguished from *Xanthorhoini* s.str. as follows (Viidalepp 2006, 2009 and unpubl.): uncus sclerotized dome- or cupola-shaped; sacculus fully fused to valvula; joint of costa and sacculus shifted ventrad; juxta as a short and broad (rounded H-shaped) sclerotized plate of specific shape (Fig. 120); a pair of sclerites dorsal to juxta present (Figs 117, 120); manica heavily spinose, shifted and fused to dorsum of juxta; transtilla sclerotized continuous bridge-shaped; subscaphium a flat plate, bifurcate basally and connected to tegumen; valve costa leg-shaped free, connected to valva basally only and fixed by a transverse, bridge-like sclerite (Fig. 117) in northern hemisphere species, fused to valvula and projecting apically in Neotropical taxa (Fig. 124); aedeagus often with a short basal keel; apophyses in female long and dilated-flattened at apex (Fig. 122); female with signum a rounded, finely dentate plate in boreal species (Fig. 122); ostium large cup-shaped; male abdominal segment differing from *Xanthorhoini* in the anterior margins in fusion of the sternite and tergite A8 into a closed ring with ventral and dorsal flaps attached (Fig. 119); valva inner wall basally membranous or emarginated against manica; subscaphium basal branches arising from tegumen; vinculum shorter than tegumen.

The genus *Euphyia* is speciose in South America, sympatrically with related genera as *Hammaptera* Herrich-Schäffer (Figs 125–129) and others.

Distribution: Neotropical, Holarctic.



**FIGURES 117–124**, Male and female genitalia and coremata of Euphyiini. 117, Male genitalia and aedeagus of *Euphyia biangulata* (Haworth); 118, abdominal segments A7, A8 and coremata of male *E. biangulata* (Haworth); 119, male genitalia of *Euphyia* sp. (Nicaragua); 120, abdominal segments A7, A8 and coremata of *Euphyia* sp. (Nicaragua); 121, female genitalia of *Euphyia* sp. (Nicaragua); 122, female genitalia of *Euphyia* sp. 2 (Nicaragua); 123, female genitalia of *Euphyia* sp. 2 (Nicaragua); 124, male genitalia of *E. porraceata* (Snellen) (Ecuador).



**FIGURES 125–129**, Male genitalia and coremata of *Hammaptera* Herrich-Schäffer. 125, Male genitalia and aedeagus of *Hammaptera* sp. (Venezuela); 126, abdominal segments A7 and A8 with coremata of *Hammaptera* sp. (Venezuela); 127, male sternite and tergite A8 of *Hammaptera* sp. (Venezuela); 128, male genitalia of *Hammaptera* sp. 2 (Ecuador); 129, male posterior abdominal segments and coremata of *Hammaptera* sp. 2 (Ecuador).

### Tribe *Xanthorhoini* Pierce, 1914

(Fig s 130–148)

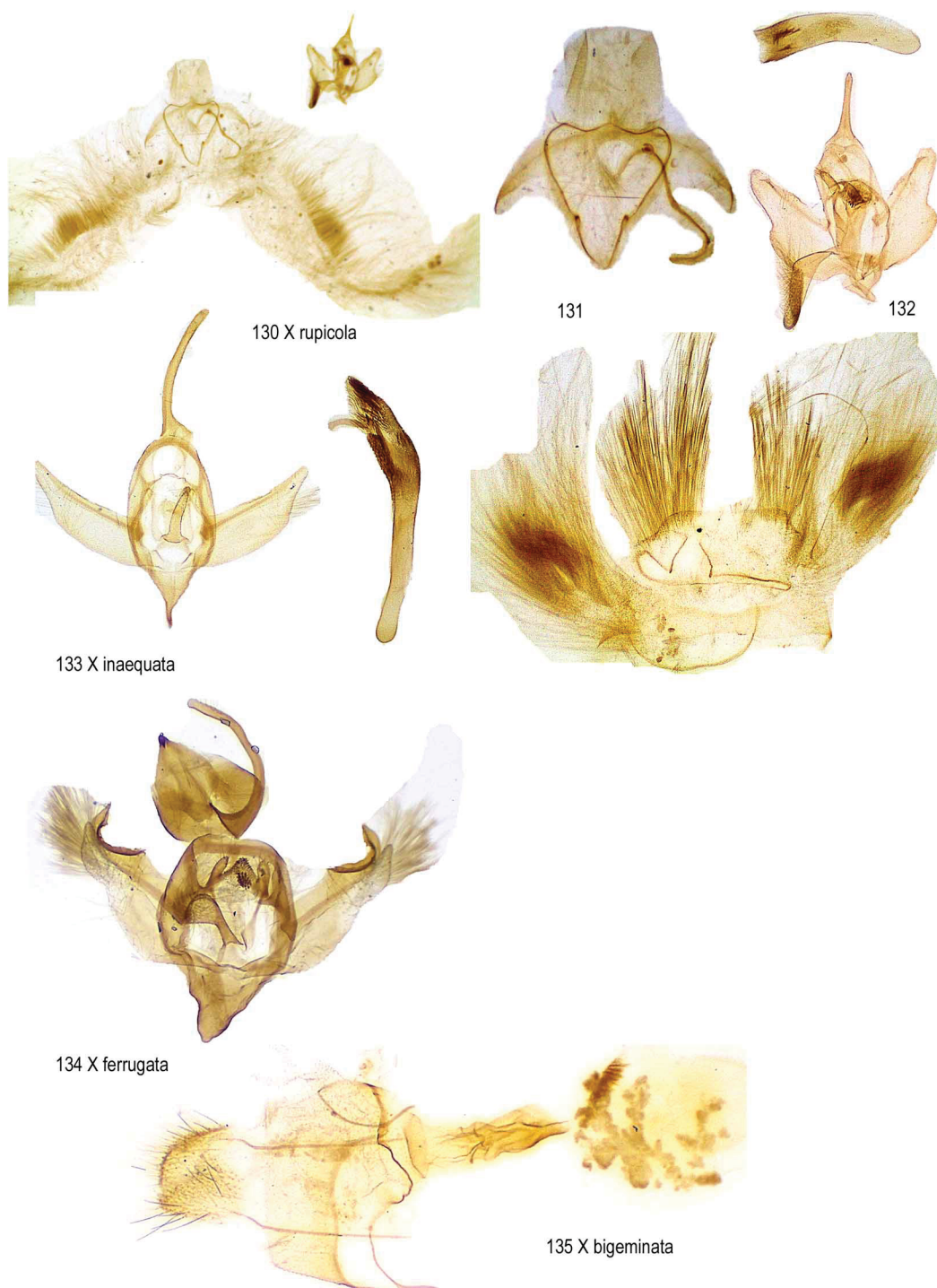
The original treatment in Pierce (1914) included *Xanthorhoe* Hübner, *Orthonama* Hübner, *Ochyria* Hübner, *Campotogramma* Stephens, *Percnoptilota* Hulst and *Mesotype* Hübner but also *Anticlea* Stephens and *Earophila* Gumpenberg (both genera without coremata) and may be interpreted different as compared with preceding Epirrhoinae: Coremata at seventh segment of male abdomen; valve costa greatly extended with projecting process; valvula reduced; calcar long with geniculate head (vestigial in some New Zealand taxa: Craw 1987); manica heavily sined; signum a pyriform band, consisting of overlapping spines; small-sized, heavily sclerotized male armatures.

Forbes (1948) stressed the characters of Xanthorhoini as follows: the straight, “erect” hind wing upper discocellular vein (mdcv, here DC1) and large coremata pencils on seventh abdominal segment of male (subsuming *Euphyia* Hübner into his genus *Xanthorhoe* Hübner).

Herbulot (1961) recombined the groups Epirrhoinae Pierce and Ortholithinae Pierce in Xanthorhoini. Holloway (1997: 190) wrote: “The presence of a large pair of coremata just distal to the eighth segment in male abdomen appears to be the most constant feature for this tribe. Though the occurrence of a calcar ... is an additional diagnostic feature...”. Holloway (loc. cit.) diagnosed the calcar as a curved process, club-like structure arising centrally from the juxta between the bases of valves. The group requires a global revision (Holloway *et al.* 1987).

Modifications in the region of fultura inferior as defined here, include: Sternite A7 is membranized to a fili-form stripe, the corresponding tergite to a bow-shaped sclerite.





**FIGURES 130–135**, Male genitalia and coremata of Xanthorhoini. 130, Size of coremata and genitalia in *Xanthorhoe rupicola* (Wollaston) (Madeira); 131, posterior abdominal segments of *X. rupicola* (Wollaston) (Madeira); 132, male genitalia and aedeagus of *X. rupicola* (Wollaston) (Madeira); 133, male genitalia, aedeagus and coremata of *X. inaequata* Warren (Madeira); 134, male genitalia of *X. ferrugata* (Clerck); 135, female genitalia of *X. bigeminata* (Christoph) (Turkmenistan).

Sternite A8 is reduced to a stripe, smooth in Holarctic species but V-shaped angulate in many southern hemisphere genera (Figs 136, 137).

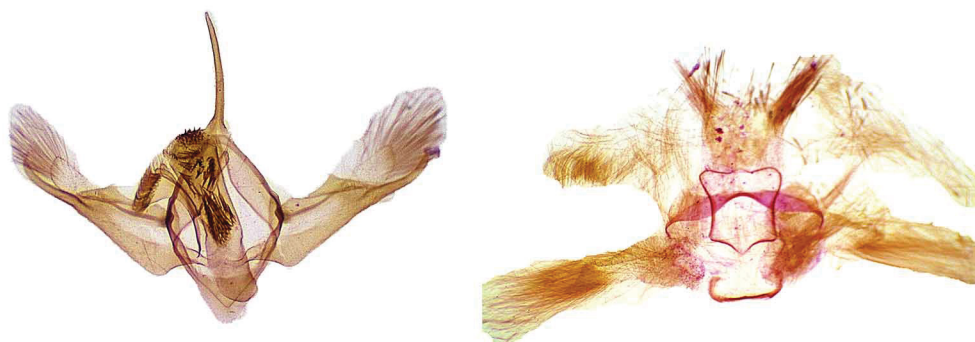
Tergite A8 usually consists of a basal stripe and dorsal semi-membranous flap (Figs 131, 136). In Rheumapterini, coremata are at the eighth segment, with both sternite and tergite dissclerotized to a slender central band (Fig. 71); labides sometimes present, on fultura, (Craw 1987), or headed on stalk.



136 *C mecynata*



137 *C sp.*



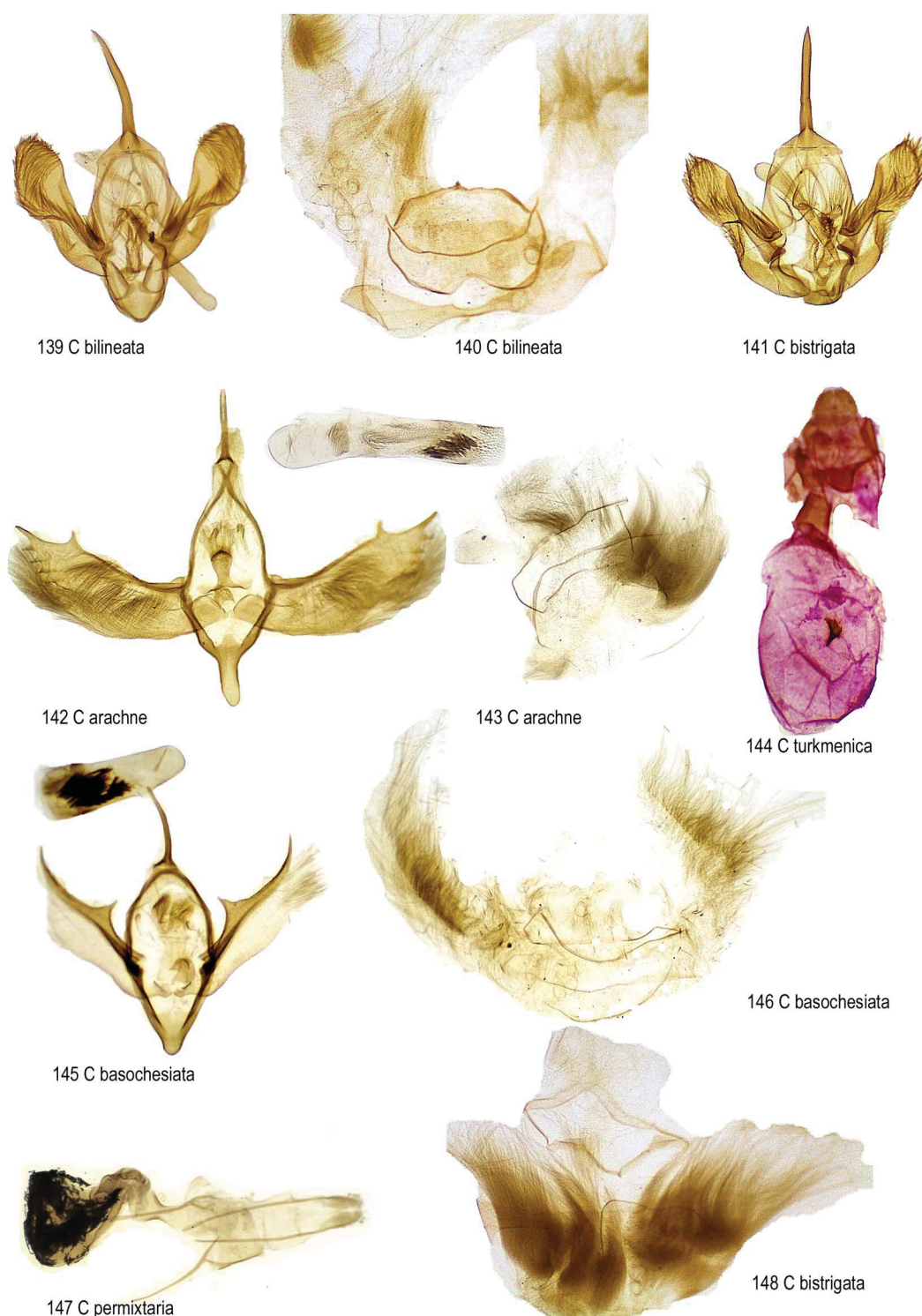
138 *E subidaria*

**FIGURES 136–138**, Male genitalia and coremata of *Chrysolarentia* Butler and *Epyaxa* Meyrick (Xanthorhoini). 136, Male genitalia and abdominal segments A7 and A8 with coremata of *Chrysolarentia mecynata* (Guenée) (Tasmania); 137, male genitalia and abdominal segments A7 and A8 with coremata of *Chrysolarentia* sp. (Australia); 138, male genitalia and abdominal segments A7 and A8 with coremata of *Epyaxa subidaria* (Guenée) (Tasmania).

The tribe as defined above is polymorphic. The seventh segment may be broad, variously modified both in south hemisphere and boreal genera (*Camptogramma* Stephens Figs 139, 140). Male genital armatures are large in some genera (*Catarhoe* Prout, Figs 142–148, *Epirrhoe*, Fig. 153). There are sclerotized longitudinal folds in epirrhine and catarhine female genitalia. *Epirrhoina* Pierce, 1914 was synonymized with Xanthorhoini by Herbulot (1961).

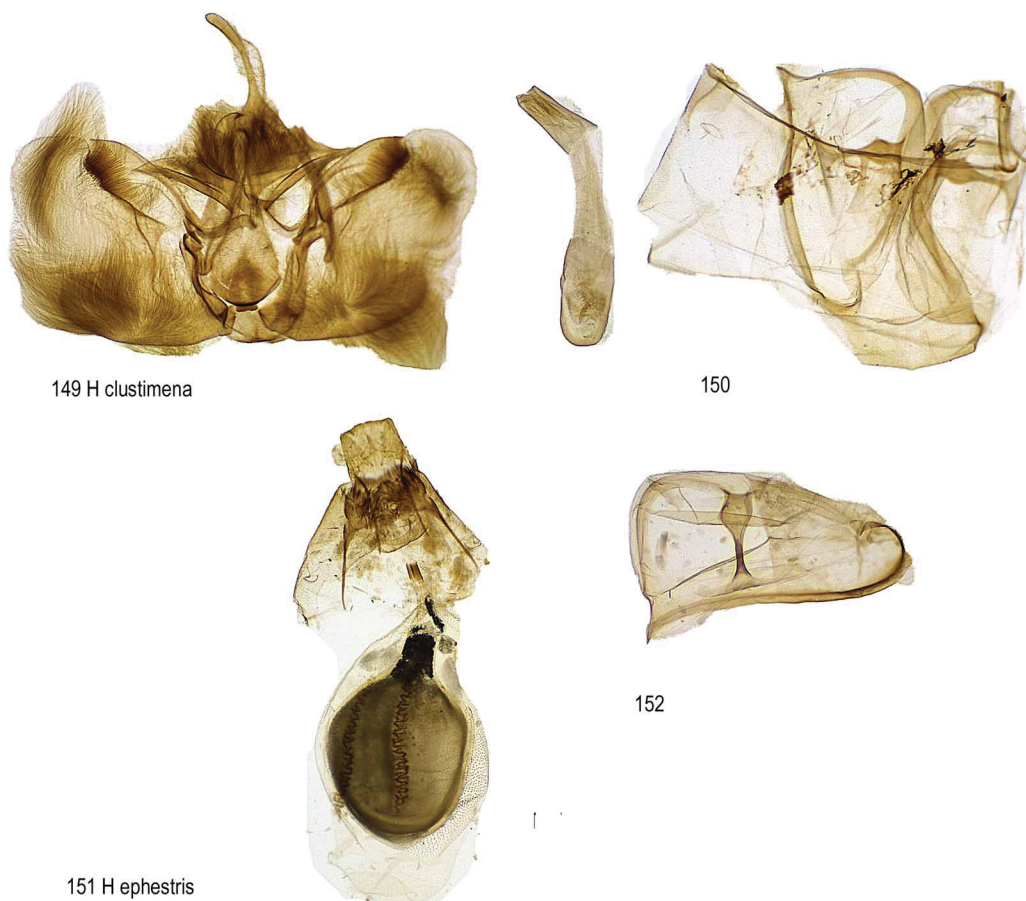
The presence of extensile coremata to the distal end of male abdomen, associated with membranization of the two last segments, is shared by Xanthorhoini, Cataclymini, Euphyiini. The presence of a medial appendage to juxta (calcar) is shared by most xanthorhine genera and the Larentiini but not Euphyiini. Female apophyses are short and weak in Xanthorhoini and Cataclymini, but not in Euphyiini.

Distribution of Xanthorhoini: all regions, tending boreal and mountainous.



**FIGURES 139–148**, male genitalia and coremata and female genitalia of *Camptogramma* Stephens and *Catarhoe* Herbulot (Xanthorhoini). 139, Male genitalia of *Camptogramma bilineata* (Linnaeus); 140, coremata of male *C bilineata* (Linnaeus); 141, male genitalia of *C. bistrigata* (Treitschke) (Sardinia); 142, male genitalia and aedeagus of *Catarhoe arachne* Wiltshire (Tadjikistan); 143, coremata of *C. arachne* Wiltshire (Tadjikistan); 144, female genitalia of *C turkmenica* (Stshetkin) (Turkmenistan); 145, aedeagus and male genitalia of *C basochesiata* (Duponchel) (Cyprus); 146, male coremata of *C basochesiata* (Duponchel) (Cyprus); 147, female genitalia of *C. permixtaria* (Herrich-Schäffer) (Armenia); 148, male coremata of *Camptogramma bistrigata* (Treitschke) (Sardinia).

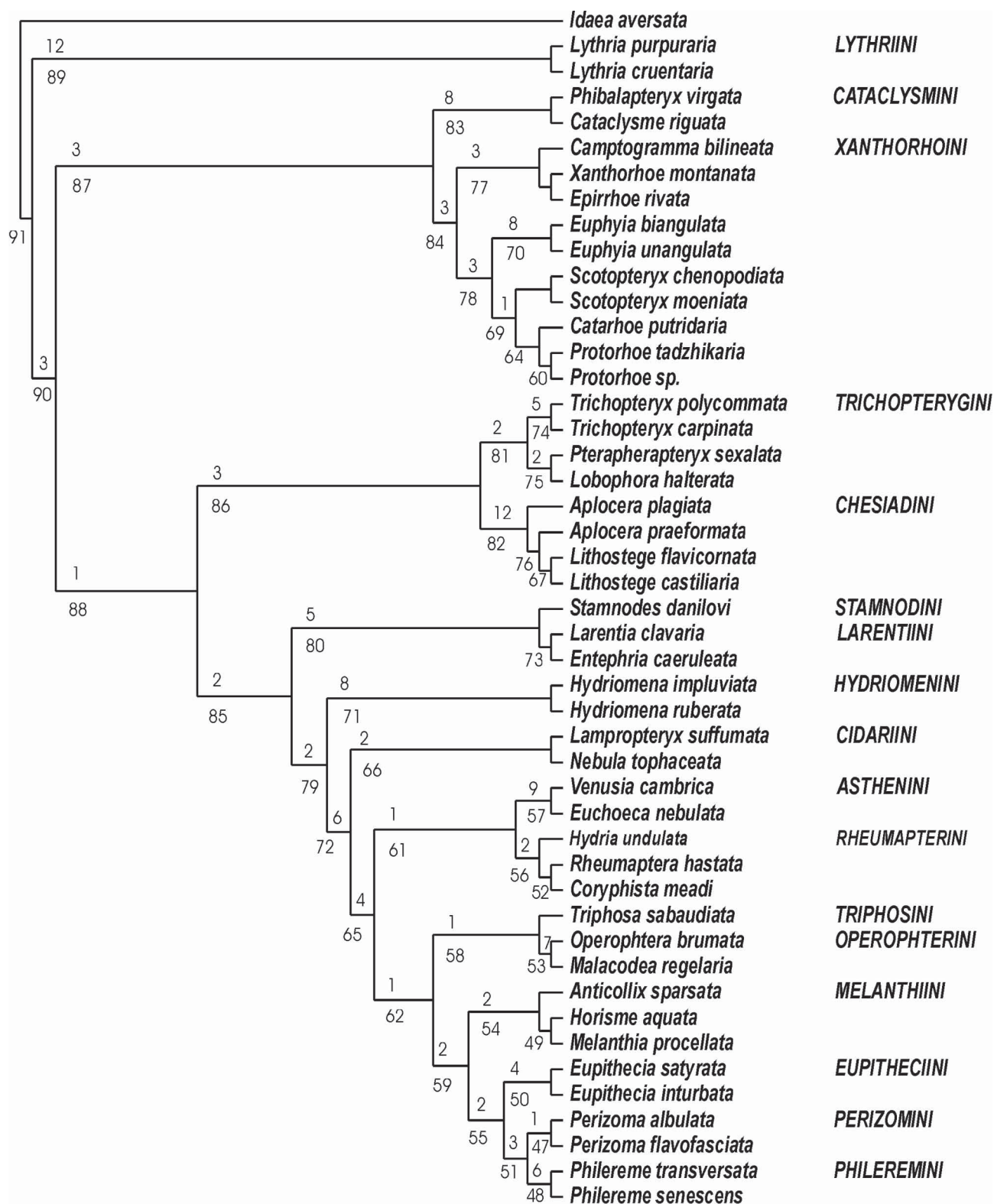




**FIGURES 149–152**, Male and female genitalia, ansa and posterior abdominal segments of *Hagnagora* Druce. 149, Male genitalia and aedeagus of *Hagnagora clustimena* (Druce) (Bolivia); 150, posterior abdominal segments of *H. clustimena* (Druce) (Bolivia); 151, female genitalia of *H. ephestris* (Felder & Rogenhofer) (Bolivia); 152, ansa of *H. ephestris* (Felder & Rogenhofer) (Bolivia).



**FIGURES 153–154**, Male genitalia of *Epirrhoe* (Hübner). 153, Male genitalia of *Epirrhoe rivata* (Hübner); 154, male posterior abdominal segments and coremata of *E. rivata* (Hübner)



Lare9 weighted tree, 795 steps, ci = 0.72, ri = 0.89.

Node numbers, below, number of character state changes above nodes

FIGURE 155, Cladogram of Larentiinae from Viidalepp (2006).

## Tribe *Cataclysmi* Herbulot, 1961

(Figs 103–108)

Herbulot (1961) separated the tribe without a diagnose. The position of Cataclysmi was defined in cladistic schemes by Choi (2006) as a subclade within Xanthorhoini, by Viidalepp (2006 unpubl.) as sister-group to Xanthorhoini s. str. The separation of Cataclysmi and Xanthorhoini was argued anew by Viidalepp (2008).

The tribe has a long list of peculiar characters: forked (*Paraplaneta*) or bifid uncus (*Cataclysmes*; *Phibalapteryx* Curtis, *Mimoclystia* Warren, (Figs 107, 103, 104); sacculus a basal sclerite to costa (shared with Euphyiini); forewing  $R_5$  stalked with  $M_1$ , areole absent (as in *Gagitodes* (Perizomini)); dark pigmentation of wings; long aedeagus with dorsal-external carina; subscaphium strongly sclerotized, forked or X-shaped (Fig. 103); costa plate-like, flat, projecting distally (shared with Xanthorhoini) sacculus projection strong, flat, nearly as long as costa; sclerite between sacculi and saccus present (possible homology with *Aplocerina*); heavy sclerotized genitalia also in female; furrowed ductus bursae; ostium cleft and fused to sternite A7; juxta shifted dorsad, from adjacent to saccus to transtilla.

Distribution: (Afrotropical), Palaearctic.

## Discussion

In an earlier cladistic analysis of the northern hemisphere larentiine tribes, inferred from morphological data sets, Viidalepp (2006, unpublished data) supported sixteen tribes as monophyletic, in the following sequence: (Cataclysmi, Xanthorhoini) ((Trichopterygini, Chesiadini) ((Stamnodini, Larentiini) (Hydriomenini (Cidariini ((Asthenini, Rheumapterini) ((Triphosini, Operophterini) (Melanthiini (Eupitheciini (Perizomini, Phileremini))))))). This cladogram (Fig. 155) was based on 129 morphological characters compiled for 38 genus-group taxa and *Idaea aver-sata* Linnaeus as an outgroup species. These 38 genus-group taxa were selected as representatives of monophyletic groups during the preceding cladistic analyses. The sequence was checked according to larval chaetotaxy data and principal trends of imago modification in the second part of the presentation (Viidalepp 2006). Morphological data, including chaetotaxy, i.e. topography of primary setae in larentiine larvae, are scarce in literature, the review by McGuffin (1958) and descriptions by M. Ahola (Mikkola *et al.* 1987) and King & Parra (2011) as examples. Author's data are based on Estonian material.

The presence of extensile abdominal coremata appeared associated with the presence of numerous (8 and more) primary setae on ventral proleg of mature larva. In addition, Hydriomenini and Stamnodini, two tribes which are most speciose in Neotropics, have more than 10 setae on abdominal proleg of larva. The tribes which are characterised by four setae on larval proleg, have also labides which arise from valve costa (Eupitheciini, Perizomini, Asthenini, Melanthiini, Phileremini, Triphosini, Rheumapterini, Operophterini, Cidariini). The extensile abdominal coremata of male sex are characteristic also for Idaeini (Sterrhinae), Azelinini (Ennominae), therefore supposed as plesiomorphic trait. Loss of abdominal coremata and reduction of larval setosity seems more common in boreal groups of Larentiinae. The sequence of larentiine tribes and arrangement of West Palaearctic genera were used for the Fauna Europaea Checklist (Hausmann *et al.* 2007) and in Forum Herbulot Homepage (Hausmann 2007).

However, cladistic analyses, especially those using the example species approach, are trustworthy concerning just these taxa and characters included. Both cladistic treatment of morphology and molecular-taxonomic analysis of Lythriini yielded trustworthy and robust trees when all the five species of *Lythria* Hübner were included in matrices (Öunap *et al.* 2009).

## A model of the taxonomic structure of the subfamily Larentiinae

Morphological features of twenty-two larentiine tribes are listed and compared. The tribes are grouped as follows: Dyspteridini, Trichopterygini, Chesiadini with subtribes Chesiadina and Aplocerina subtr. nov., Eudulini, Eupitheciini; Asthenini, Melanthiini, Perizomini, Phileremini, Rheumapterini, Triphosini, Operophterini, Erateinini, Cidariini, Stamnodini, Solitaneini, Hydriomenini, Larentiini, Scotopterygini, Xanthorhoini, Euphyiini; Cataclysmi. The tribe Heterusiini Warren is not examined due lack of material.



Four tribes the Dyspteridini, Chesiadini, Erateinini and Trichopterygini, have the shape and venation of wings modified. The Trichopterygini has the widest spectrum of its morphological characters. According to Yamamoto and Sota (2007), the tribe is placed as the sister-taxon to all other larentiines. Here the deeply dimorphic Dyspteridini is placed as the most basal tribe of larentiines according to the results published by Sihvonen *et al.* (2011).

The Erateinini has some affinities to the Cidariini and is suggested to be placed basal to this tribe.

The Chesiadini has no modification to the region of the fultura inferior and juxta but long or very long projections to the base of valve costa and has medial ornamentation of the valva. Two subtribes Chesiadina and Aplocerina are well characterized.

There are two different sets of tribes characterized by complicated structures derived for interspecific chemical communication, which are localized on abdomen or valvae.

The posterior abdominal segment or (usually) segments of male are desclerotized and bear extensile coremata between segments A7 and A8 in the xanthorhoine lineage, in the tribes Cataclysmiini, Xanthorhoiini and Euphyiini. The saccular ornamentation of the valva is reduced in Xanthorhoiini and Euphyiini, the costal ornamentation present.

The Scotopterygini, with its tegumen and vinculum often jointed, not fused, is placed as a basal sister taxon to others with coremata on male abdominal segments A7 and A8. It differs from Xanthorhoiini in the desclerotization of the male abdominal segment A8 only, by short coremata.

The tropical genus *Piercia* Prout and Central Asian *Kauria* Viidalepp share with a heavy sclerotization of genitalia, the presence of costal and saccular ornamentation of valva with *Scotopteryx*. An apomorphic character for the both abovementioned genera is the presence of a pair of strong hamuli arising from lateral pockets of juxta (Figs e.g. in Krüger 2005).

Some different trends in the modification of male genitalia occur within the Holarctic Xanthorhoiini (incl. Epirrhoinae Pierce which was synonymized with Xanthorhoiini by Herbulot (1962)), whereas some Australian genera possess male abdominal segments A7 and A8 that are less membranized and the sternite A8 is often V-shaped angulate.

The Euphyiini, with the male abdominal segment A8 fused ring shaped basally and the sclerotization of the region of fultura inferior is specific. In the Xanthorhoiini the eighth sternite and tergite are separated and the fultura inferior has membranized ornamentation.

The Eupitheciini, Asthenini, Melanthiini, Rheumapterini, Perizomini and Operophterini have derived labides and should be grouped together. Male eversible coremata are positioned between the last abdominal segment and bases of valvae.

The labides arise from the valva base, branching dorsad and towards the “neck” of juxta in the Eupitheciini, Perizomini, Melanthiini. These three tribes have distal membranes of labides fused. Heads of labides are simpler in the Asthenini and Rheumapterini. In some aspects, the Melanthiini constitute a relatively robust sub-group of the Eupitheciini as suggested by Holloway (1997).

The Larentiini, which have been previously affiliated with the Xanthorhoiini (Holloway 1997), however, have ornamentation to fultura inferior and lack coremata. The tribe has valval structure and vestiture as in the Cidariini, Eudulini and Hydriomenini, and projections from juxta similar to those in Xanthorhoiini.

The Cidariini, Hydriomenini s. str., Eudulini have labides arising from more or less large, membraneous juxta and sacculus fused to valvula (except for conifer-feeding genera *Thera*, *Heterothera* Inoue have saccular ornamentation to valva).

The Cidariini is represented by at least four different groups of genera in the Holarctic fauna. From a variety of Neotropical genera, unassigned to tribes at present, some (*Brabiroides* Guenée) share genital characters with the Cidariini, while some others should possibly be assigned to tribes of their own in future.

In particular, Trichopterygini, Eupitheciini and Xanthorhoiini are polymorphic and widespread in all biogeographical regions. Chesiadini, Rheumapterini, Asthenini, Melanthiini, also widespread, are thus most speciose in one of regions—the former two in the Palaearctic, the latter two occur in the Oriental, Afrotropical and Australian regions. Hydriomenini, Stamnodini and Euphyiini are relatively monomorphic tribes, richly represented in South America but barely reaching into the Holarctic, Dyspteridini, Eudulini and Erateinini barely reach North America from South America.

Perizomini and Solitaneini have a Palaearctic distribution, while Operophterini is Holarctic.

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## Appendix 1. Larentiinae genera and subgenera examined.

Dyspteridini: *Dyspteris* Guenée, *Celonoptera* Lederer.

Trichopterygini: *Heterophleps* Herrich-Schäffer, *Carige* Walker, *Tyloptera* Christoph, *Brabira* Moore, *Leptostegna* Christoph, *Rhopalodes* Guenée, *Ptygmatophora* Gumpfenberg, *Lobophora* Curtis, *Pterapherapteryx* Curtis, *Epilobophora* Inoue, *Acasis* Duponchel, *Nothocasis* Prout, *Oulobophora* Staudinger, *Episauris* Rebel, *Trichopteryx* Hübner, *Cladara* Hulst, *Esakiopteryx* Inoue, *Trichopterigia* Hampson, *Tatosoma* Butler, *Sauris* Guenée, *Trip-tiloides* Parra & Santos. (unnamed genera)

Chesiadini (Chesiadina): *Chesias* Treitschke, *Chesistege* Viidalepp, *Lithostege* Hübner.

*Schistostege* Hübner;

Chesiadini (Aplocerina): *Amygdaloptera* Gumpfenberg, *Odezia* Boisduval, *Carsia* Hübner, *Docirava* Walker, *Aplocera* Stephens.

Eudulini: *Eudulophasia* Warren, *Eubaphe* Hübner.

Eupitheciini (Chloroclystina): *Gymnoscelis* Mabille, *Chloroclystis* Hübner, *Rhinoprora* Warren; *Prorella* Barnes & McDunnough, *Microdes* Guenée.

Eupitheciini (Eupithecina): *Eupithecia* Curtis, *Phrissogonus* Butler, *Micrulia* Warren, *Mnesiloba* Warren.

Asthenini: *Asthenia* Hübner, *Hydrelia* Hübner, *Euchoeca* Hübner, *Venusia* Curtis, *Nomenia* Pearsall, *Hastina* Moore.

*Poecilasthena* Warren, *Minoa* Treitschke, *Eois* Hübner.

Melanthiini: *Bundelia* Viidalepp, *Zola* Warren, *Melanthia* Duponchel, *Coenocalpe* Hübner, *Horisme* Hübner, *Collix* Guenée, *Herbulotia* Inoue, *Anticollix* Prout, *Echthrocollix* Inoue, *Eccymatoge* Prout-

Perizomini: *Pseudobaptria* Inoue, *Mesotype* Hübner, *Martania* Mironov, *Perizoma* Hübner, *Gagitodes* Warren.

Rheumapterini: *Hospitalia* Agenjo, *Rheumaptera* Hübner, *Hydria* Hübner, *Xenospora* Warren, *Eutriphosa* Gump-  
penberg, *Coryphista* Hulst.

Triphosini: *Triphosa* Stephens, *Strepsizuga* Warren, *Speluncaris* Bruand, *Pareulype* Herbulot,

Phileremini: *Philereme* Hübner.

Operophterini: *Epirrita* Hübner, *Malacodea* Tengström, *Operophtera* Hübner.

Erateinini: *Erateina* Doubleday.

Cidariini: *Pljushtshia* Viidalepp & Kostjuk, *Heterothera* Inoue, *Protothera* Viidalepp, *Praethera* Viidalepp, *Pennithera* Viidalepp, *Thera* Stephens, *Lampropteryx* Stephens, *Xenortholita* Inoue, *Cosmorhoe* Hübner, *Almeira* Agenjo, *Nebula* Bruand, *Colostygia* Hübner, *Calostigiodes* Aubert, *Eulithis* Hübner, *Gandaritis* Moore, *Lobogonodes* Bastelberger, *Hyaterura* Warren, *Eustroma* Hübner, *Trichobaptria* Prout, *Trichodezia* Warren, *Polythrena* Guenée, *Calleulype* Warren, *Eucosmabraxas* Prout, *Ecliptopera* Warren, *Electrophaes* Prout, *Chloroclysta* Hübner, *Dysstroma* Hübner, *Cidaria* Treitschke, *Plemyria* Hübner,

Stamnodini: *Stamnodes* Guenér, *Callipia* Guenée.

Solitaneini: *Solitanea* Djakonov, *Baptria* Hübner.

Hydriomenini: *Hydriomena* Hübner.

Larentiini: *Idiotephria* Inoue, *Antilurga* Herbulot, *Earophila* Gump-  
penberg, *Anticlea* Stephens, *Mesoleuca* Hübner, *Pelurga* Hübner, *Pseudentephria* Viidalepp, *Kuldsha* Alphéraky, *Kyrtolitha* Staudinger, *Plesioscotosia* Viidalepp, *Photoscotosia* Warren, *Larentia* Treitschke, *Entephria* Hübner, *Neotephria* Prout, *Spargania* Guenée.

Scotopterygini: *Scotopteryx* Hübner.

Euphyiini: *Euphyia* Hübner, *Hammaptera* Herrich-Schäffer.

Xanthorhoini: *Chrysolarentia* Butler, *Epyaxa* Meyrick, *Psychophora* Kirby, *Costaconvexa* Agenjo, *Orthonama* Hübner, *Nycterosea* Hulst, *Protorhoe* Herbulot, *Catarhoe* Herbulot, *Juxtephria* Viidalepp, *Camptogramma* Stephens, *Glaucorhoe* Herbulot, *Xanthorhoe* Hübner, *Epirrhoe* Hübner, *Austrocidaria* Dugdale, *Visiana* Swinhoe

Cataclymini: *Phibalapteryx* Stephens, *Cataclysmes* Warren, *Paraplaneta* Warren, *Piercia* Janse, .

Heterusiini